

THE POSTCRANIAL SKELETON OF *HETERODONTOSAURUS TUCKI*  
(REPTILIA, ORNITHISCHIA) FROM THE STORMBERG OF  
SOUTH AFRICA

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(With 23 figures, 1 table and 1 appendix)

[MS. accepted 30 August 1979]

ABSTRACT

*Heterodontosaurus tucki* (SAM-K1332), from the Upper Red Beds of the Stormberg Series, comprises the only known complete postcranial skeleton of an early ornithischian dinosaur. It is characterized by: length just over 1 m; a short presacral, especially dorsal, region; six fused sacrals; ossified tendons only in the dorsal region; humerus with large deltopectoral crest and entepicondyle; ulna with an olecranon process; nine carpal elements; three functional, parallel, manual digits; elongated tibiofibula; functional tibiotarsus and tarsometatarsus; small, robust prepubis; and ischium without an obturator process.

*H. tucki* was bipedal but probably capable of slow quadrupedal progression. The hand was a grasping organ and the forelimb possessed powerful flexor musculature. The hind limb was abducted and protracted, but definitely not parasagittal nor vertical. The tail was not rigid.

*H. tucki* differed in many important characters from fabrosaurids, indicating a long period of ornithischian evolution still unknown. Resemblances are found to Jurassic-Cretaceous ornithopods and non-ornithopods, particularly small Ceratopsia. Ornithopods are redefined as only those ornithischians having an obturator process. *H. tucki* is classified as a non-ornithopod of unknown subordinal status. It argues for the existence of a non-ornithopodous radiation possibly ancestral to some later non-ornithopods.

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## INTRODUCTION

All known Late Triassic ornithischians are classified either as fabrosaurids or heterodontosaurids. The family Fabrosauridae has recently been surveyed, in part, by Galton (1978). In this family he included *Fabrosaurus australis* Ginsberg, 1964, *Echinodon* Owen, 1861, *Nanosaurus* Marsh, 1877, and *Lesothosaurus diagnosticus* Galton, 1978 gen. et sp. nov. This last is the fabrosaurid material described by Thulborn (1970a, 1972) as *Fabrosaurus australis*; it is the only specimen of the above with sufficient postcranial material for comparison with *Heterodontosaurus tucki*.

The family Heterodontosauridae includes *Heterodontosaurus tucki* Crompton & Charig, 1962, *Lycorhinus angustidens* Haughton, 1924, *Abrictosaurus consors* (Thulborn, 1974) *Lanasaurus scalpridens* Gow, 1975, *Geranosaurus atavus* Broom, 1911, and *Pisanosaurus mertii* Casamiquela, 1967. *P. mertii* has been classified as a hypsilophodontid by Galton (1972) but as a heterodontosaurid by Bonaparte (1976). *Abrictosaurus consors* (Hopson 1975) comprises the material which Thulborn (1974) described as *Lycorhinus consors* (specimen B54, Department of Zoology, University College, London). But apart from SAM-K1332, the specimen described here, little heterodontosaurid postcranial material exists.

Previous discussions of *Heterodontosaurus* have dealt primarily with its cranial and dental anatomy (Crompton & Charig 1962; Charig & Crompton 1974). Little attention was given to the available postcranial skeleton (but see Santa Luca, Crompton & Charig 1976), though it is the most complete of any known Triassic ornithischian. This is the first study to describe heterodontosaurid morphology in detail; the purpose is to present a thorough analysis of the postcranial anatomy and of its implications for ornithischian phylogeny.

## HISTORICAL SURVEY

Though no detailed study of *Heterodontosaurus* has previously appeared, it has been discussed frequently in the press. Most of the controversy has centred around the familial status and generic synonymies of *Heterodontosaurus*. Crompton & Charig's (1962) announcement of the first *Heterodontosaurus* skull described the dentition and diagnosed the specimen as ornithischian. After short comparisons with iguanodonts and hadrosaurs, they *provisionally* assigned *Heterodontosaurus* to the suborder Ornithopoda but not to any family within that suborder.

Romer (1966: 370) made it the monotypic genus of the family Heterodontosauridae. However, Thulborn (1970a: 430) assigned it to the Hypsilophodontidae in his study of a fabrosaurid skull, but he gave no reasons for so doing. Subsequently, the systematic position of *Heterodontosaurus* became greatly confused as Thulborn (1970b, 1974) described another South African ornithischian as congeneric with *Lycorhinus angustidens* Broom, 1911, and then argued that the



Fig. 1. *Heterodontosaurus tucki* (Crompton & Charig). SAM-K1332 in left lateral view. The skull and mandible in this photograph are casts of the original.



name *Heterodontosaurus* was but a junior synonym of *Lycorhinus* and therefore not valid.

In answer to this, Charig & Crompton (1974) and Hopson (1975) adequately demonstrated that generic distinctions in the dentition did exist between *Heterodontosaurus* and *Lycorhinus*. Furthermore, Galton (1972), Charig & Crompton (1974), and Hopson (1975) have all shown that *Heterodontosaurus* is sufficiently distinct from the Hypsilophodontidae to warrant separate familial status. Thulborn (1974) later accepted a familial distinction, but continues to refer to this genus as '*Lycorhinus*' (Thulborn 1978).

Because of its dentition and some of its cranial characters, *Heterodontosaurus* has always been considered a rather specialized ornithischian. From this Thulborn (1970a, 1971a, 1972, 1974) has inferred that heterodontosaurids were a short-lived evolutionary divergence from the basal ornithischian stock. In a previous publication Santa Luca *et al.* (1976), only assumed that *H. tucki* itself could not be ancestral to later ornithischians. This hypothesis will be thoroughly examined at the end of this study since some important similarities in the post-cranial skeleton of *H. tucki* and later ornithischians do exist.

The result of previous work has been to clarify the familial and generic status of *Heterodontosaurus*. However, the question of the subordinal status of *Heterodontosaurus* has never been examined. It has simply been standard practice to classify all bipedal ornithischians as Ornithopoda. This is unsatisfactory for some bipedal ornithischians (e.g. pachycephalosaurs) and so the question of subordinal status will be taken up in the discussion.



Fig. 2. *H. tucki*. SAM-K1332. Skull, right lateral view.  $\times 1$ .



## MATERIAL

The specimen described here (South African Museum K1332) is on loan to the Museum of Comparative Zoology, Harvard University. It was discovered in December 1966 in the Upper Red Beds of the Stormberg series, about 1 770 m above sea-level on the northern slopes of Krommespruit Mountain near Voisana in the District of Herschel, Republic of South Africa. The specimen consists of a virtually complete and articulated skeleton of an adult ornithischian dinosaur (Figs 1-2). The precise extent of preservation of each skeletal element has been noted at the beginning of the descriptive sections. A complete list of measurements is provided in the appendix.

Comparisons have been made with a cross-section of published ornithischian material. This includes ankylosaurs (Coombs 1978a, 1978b), *Camptosaurus* (Gilmore 1909), ceratopsians (Hatcher, Marsh & Lull 1907; Lull 1933), *Fabrosaurus* (Thulborn 1972; Galton 1978), hadrosaurs (Lull & Wright 1942), *Hypsilophodon* (Galton 1974), *Iguanodon* (Hooley 1925), *Microceratops* (Maryańska & Osmólska 1975), pachycephalosaurs (Maryańska & Osmólska 1974), *Protiguanodon* and *Psittacosaurus* (Osborn 1923, 1924), *Protoceratops* (Brown & Schlaikjer 1940), stegosaurs (Gilmore 1914), and *Thescelosaurus* (Gilmore 1915).

DESCRIPTION OF *HETERODONTOSAURUS TUCKI*

## VERTEBRAL COLUMN

The vertebral column of *Heterodontosaurus* is virtually complete and in articulated condition. However, it has been left in a bed of matrix and only the left lateral surfaces of the vertebrae are generally visible (Fig. 3); a few of the vertebral bodies, in the anterior dorsal region, can be seen from the right side (Fig. 4). In the presacral column, the most notable absence is the atlas which cannot be reconstructed from the few fragments which remain; however, the axis is exceptionally well preserved. The transverse processes of the posterior cervicals are cracked so the precise angle of the processes relative to the neural arch is uncertain. The anterior part of the centrum of C9 is missing, thus the shape of this centrum and its effect on curvature in the neck are indeterminate. The posterior cervical and the dorsal ribs overlay these vertebral bodies and obscure their structure. The most severe deformation is in the middle and posterior dorsals. Here the neural arches are collapsed downwards over the centra; the transverse processes, instead of being horizontal, are now flush against the centra and point downward. The ilia have been squeezed together, displacing the sacral ribs. The caudal vertebrae are the best preserved but are also embedded in matrix (Figs 6, 8) so only the left lateral surface is visible.

*Cervical vertebrae* (Figs 1, 3, 5A)

The cervical vertebrae of *H. tucki* can be divided into two groups based on serial changes in centrum and in neural arch shape. C2-5 have longer centra,

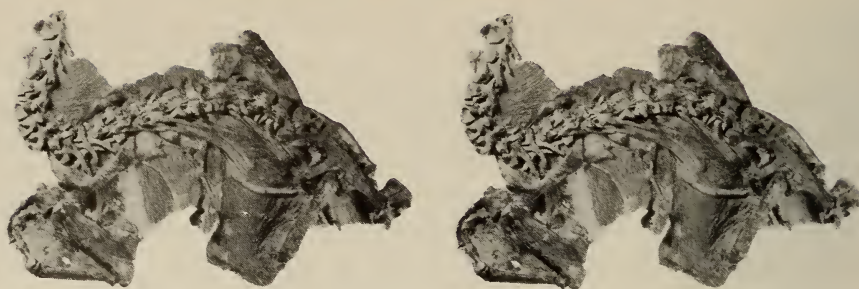


Fig. 3. *H. tucki*. Stereophotograph of main matrix block, left side. Scale = 5 cm.

longer neurocentral junctions (10–11 mm) and more widely separated pre- and postzygapophyses. Each centrum has a moderate ventral keel, concave in lateral outline, which is not strongly differentiated from the centrum itself. The axis has a rather more elongate centrum with a less marked lateral concavity and ventral keel than the other anterior cervicals. The odontoid process is 7,5 mm long. C6–9 have shorter centra, narrower neurocentral junctions (decreasing from 8 mm in C6 to 5 mm in C9), more closely apposed pre- and postzygapophyses and much more strongly developed diapophyseal processes. The keeling and concave ventral outline are more pronounced in C6–9. Furthermore, a ridge outlines the anterior and posterior intercentral margins. The anterior ridge continues up the side of the centrum and joins the parapophyseal prominence. The posterior ridge continues along the ventral margin of the centrum. These ridges outline a much deeper concavity below the parapophyses in C6–9 than in C2–5. They also increase the transverse width of the ventral keel which is narrow and sharp in C2–5, but flat and several millimetres wide in C6–9. While some of these distinctions typify the cervical vertebrae of other ornithischians (e.g. *Hypsilophodon*), the division into two groups is more pronounced in *H. tucki*.

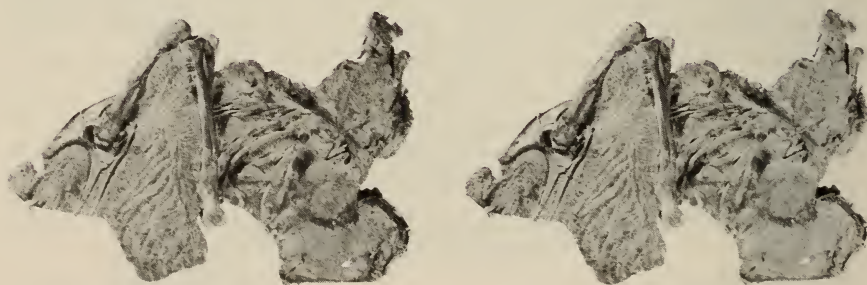


Fig. 4. *H. tucki*. Stereophotograph of main matrix block, right side. Scale = 5 cm.

Only two features of the cervical centra do not show the dichotomous variation noted above. First, the height of the centra is approximately constant throughout the series. Second, the absolute position of the parapophysis is constant in all the cervical vertebrae. The position of the diapophysis varies but not in the fashion noted above for the cervical centra: in C3-5 (the axis has no rib facet) it lies just above and behind the parapophysis, but the distance between the two facets progressively increases so that the diapophysis lies at the level of the zygapophysis on C7 and above that level on C8 and C9.

Three different kinds of neural spines are found in successive groups of cervical vertebrae: C2, 3, 4; C5, 6; C7, 8, 9. The neural arch of the axis has a very prominent spine, the long axis of which is almost horizontal, parallel to the long axis of the centrum. The arch is lateromedially compressed except at the posterior ventral margin. Here the arch develops two lateral processes or flanges; these extend from the distal tip of the arch anteriorly and inferiorly to the postzygapophyses. The neural spines of C3 and 4 are successively smaller versions of this form. C5 and 6 have small, narrow spines which project anteriorly and dorsally between the postzygapophyses of the preceding vertebra. The spine of C4 is inclined about  $45^\circ$  to the horizontal, C5 about  $30^\circ$ . The spines of C7-9 are narrow vertical processes; in C7 and 8 the tip of the spine is broken and the height uncertain; in C9 it rises about 7 mm above the level of the zygapophyses.

The orientation and position of the zygapophyses also vary in the cervical region. The prezygapophyses of the axis for articulation with the atlantal neural arch are flat and face laterally. The transverse axis of the joint is horizontal at C2/3, but it becomes successively more angulated until at C6/7 it is about  $70^\circ$  above the horizontal. The zygapophyseal joints of C7/8 and C8/9 are covered by matrix, but the transverse axis of C9/D1 is less erect than the axis of C6/7. The transverse axis is horizontal again at the D2/3 articulation (see D3/D4 in Fig. 5B).

Since the distance between the pre- and postzygapophyses of any single vertebra varies with the length of the centrum, the zygapophyses are closer together in the posterior than in the anterior group of cervical vertebra.

In the cervical series, the anterior and posterior surfaces of the centra are not perpendicular to the long axis of the centrum. Thus, the centra of C3 and 4 have a parallelogram-shaped profile; those of C5 and 6 are approximately rectangular, those of C7 and 8 trapezoidal (that of C9 is indeterminate). The differently shaped centra, when articulated, automatically impart a curvature to the neck.

Though facets for the cervical ribs begin with C3, only the ribs of C4, 5, 8 and 9 are preserved or worked out of matrix (Figs 1, 3), but this is sufficient to infer the structure of the entire series. The ribs of C3-5 are alike, being very short with capitular and tubercular processes of about equal length; both arms are equally divergent from the axis of the rib shaft and so form a Y. The rib of C9 (Fig. 5A) is incomplete distally, the preserved portion is 70 mm long; the



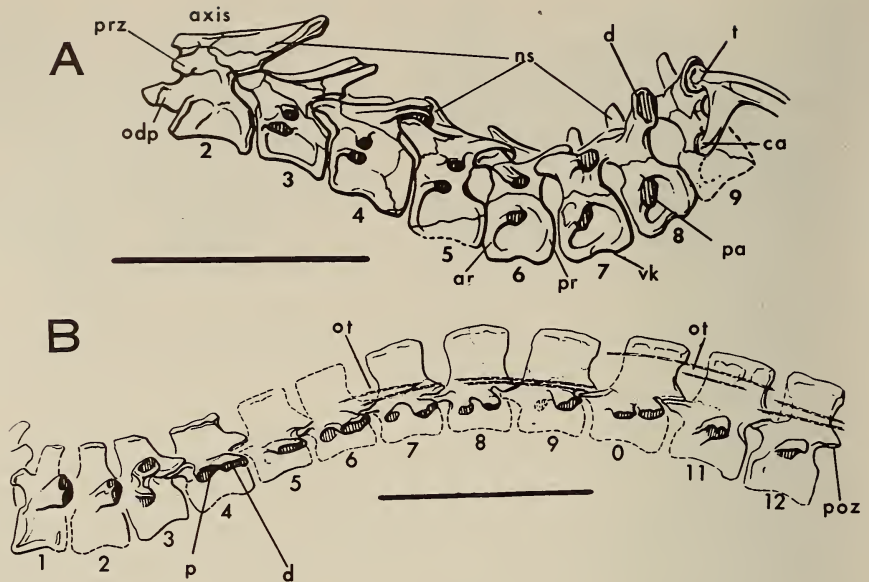


Fig. 5. *H. tucki*. A. Cervical vertebrae, left lateral view, atlas missing. B. Dorsal vertebrae, left lateral view. Scales = 5 cm.

tubercular process (6 mm long) is only half the length of the capitular process (12 mm). The tubercular process is not divergent from but lies on the long axis of the rib shaft; the head is flattened anteroposteriorly and bony excrescences indicate a strong attachment to the diapophysis. Comparable ridges are found on the diapophyses and these are especially well developed on C8 and 9. The capitular process of C9 diverges at about  $60^\circ$  from the long axis of the shaft; its head is rounded and marked by a bony ridge along only the anterior margin of the articular facet.

#### *Dorsal vertebrae* (Figs 1, 3, 5B)

Several features of the tenth vertebra indicate that it is the first dorsal; counting thus, there are then 12 dorsal vertebrae. Most importantly, compared to C6–9, the tenth centrum is elongated and has a longer neurocentral junction; the intercentral margins are not raised into strong ridges and the ventral keeling is considerably smaller.

However, the first three dorsals are, in some features, intermediate between the posterior cervicals and the remaining dorsals. The presence of a small ventral keel is an intermediate condition in that the succeeding dorsals have none. The level of the zygapophyses above the centrum decreases gradually in the first three dorsals from their position high above the centrum in the posterior cervicals (D1, Fig. 5B) to just above the centrum in most of the other dorsals (D3/4, Fig. 5B). The angle of inclination of the zygapophyseal facets gradually

decreases from D1 so that it is horizontal between D3 and 4. The diapophyses and transverse processes also become lower in the first three dorsals so that on D3 they are immediately above the parapophysis and connected to it by an oblique crest. Finally, the neural spines of the first three dorsals change from a very narrow-based process to a long-based process, about as long as the centrum itself.

D4–10 may be considered typical dorsal vertebrae. The centra are rectangular in lateral outline (the outlines were determined by radiograph for Figure 5B); consequently, the shape of the centra does not impart a curvature to the dorsal region. The centra lack the strongly marked vertical ridges on the intercentral margins seen in the posterior cervicals. The transverse processes lie approximately at the same level as the zygapophyses; furthermore, the two rib facets also lie on this level, the parapophyses (having risen completely off the centrum) on the ventromedial surface and the diapophysis on the lateral surface of the transverse process. The transverse processes are horizontal and angled posteriorly. In D6–10 the transverse process becomes bifid: that is, an incisure develops between that part carrying the parapophysis anteriorly and the part carrying the diapophysis posteriorly. The two rib facets are closer together in the posteriormost dorsals, still divided in D11 but completely merged into a single facet in D12.

While orientation of the zygapophyseal facets varies with position in the dorsal series, exact orientation is unknown because the neural arches were broken just above the centra and displaced ventrally in most of the middle dorsals. The transverse processes were also broken and folded downward, so as to lie in contact with the lateral surface of the centra. Only the processes of D3, 4, 5, 11 and 12 retain their original horizontal orientation; thus, only in these vertebrae can the orientation of the zygapophyses be determined. The facets between D3/4 and D4/5 are horizontal and those between D10/11 and D11/12 are inclined at about 45°. In the other vertebrae, if the transverse processes were restored to their horizontal position, then the inclination of the facets would also be about 45°, similar to that of D11 and 12.

The height of the zygapophyses on the neural arch decreases in the first three dorsals; but from D4–10 the height is indeterminate since the neural arches were displaced ventrally as described above. In D11 the prezygapophysis is 4–5 mm above the centrum, the postzygapophysis about 10 mm above this level. The zygapophyses of D12 are about 7 mm above the centrum.

The size and shape of the neural spine vary throughout the dorsal region. The precise height in D4–9 is uncertain, but the spines are clearly antero-posteriorly elongated at both the base and vertex. The height of the spines above the zygapophyses is about 10 mm in D3 and 14 mm in D12. The difference in height between D3 and D12 is actually greater because the zygapophyses themselves articulate at a higher level in the more posterior dorsal vertebrae.

The ribs of the transitional dorsals differ from those of the posterior cervicals only in having shorter tubercular and capitular processes. Total rib

length is indeterminate: the preserved part of dorsal rib 3? is 90 mm long. In the remaining dorsal ribs except the last, the tubercular process is so reduced that the tuberculum lies on the dorsal surface of the rib a short distance behind the capitulum. A line connecting capitulum and tuberculum makes a  $45^\circ$  angle with the proximal part of the shaft. The last dorsal rib is very short and has a single head which articulates with a reduced transverse process.

*Sacral vertebrae* (Figs 3, 7A)

The sacrum consists of six vertebrae, the centra of which are completely fused. Only a few details about the structure of the sacrum can be obtained since the sacrum is only partially exposed (and only on the left side).

Sacra 1 and 2 articulate with the anterior iliac process. The transverse processes of S1 and 2 resemble those of D12: they are short, horizontal, dorso-ventrally flattened and arise from the middle of the centrum. The first two sacra do not have typical sacral ribs which cover a large portion of the lateral central surface; rather, the ribs connect the transverse processes with the ilia. The prezygapophyses of S1 are exactly like those of D12, the transverse and anteroposterior axes angled about  $45^\circ$  to the horizontal. The prezygapophyses of S2 are completely obscured by matrix. The neural spines are as high as those of the posterior dorsals but narrower; D12 resembles S1 and 2 in this last respect more than it does D7-11.

S3 articulates with the ilia immediately dorsal and anterior to the pubic peduncle. The structure of the sacral rib is indeterminate since the centrum has a vertical fracture along which it has sheared; thus, only the point of articulation is clear, but not the shape of the bones forming it. Dorsally, only the spinous portion of the neural arch is visible: it is anteroposteriorly longer than that of S1 and 2.

In dorsal view only the basal part of the neural spine of S4 is visible, the dorsal tip being eroded away. The remaining portion resembles that of S3. S5 has an anteroposteriorly elongated transverse process which seems to be continuous with a ventrolateral projection from the centrum; this may indicate a true sacral rib. S6 has a narrow transverse process which angles caudally and meets the posterior iliac process.

The ventral surface of each centrum is concave anteroposteriorly; it is somewhat flattened transversally in S1-3 but has a slight ridge in S5 and 6.

Ossified tendons are found on the sides of the neural spines beginning abruptly at D4 (Figs 1, 3). They continue throughout the dorsal series and are found on the sides of the sacral neural spines. They disappear at S5 or 6 and are not found at all posterior to the sacrum.

*Caudal vertebrae* (Figs 6, 7B-C, 8-9)

The caudal series is not complete, but a total of 28 vertebrae remain. The first 12 are preserved in two separate but contiguous blocks of matrix. A further block contains another group of 16 articulated caudals. The number of vertebrae





Fig. 6. *H. tucki*. Stereophotograph of caudal vertebrae 3-12, left lateral view. Note distal portions of ischium and postpubic rod in lower left corner of matrix block. Scale = 5 cm.

that would bridge the gap between the two groups can be estimated by comparing the mid-central heights of the two vertebrae at the ends of the gap. (This measure seems to decrease uniformly from anterior to posterior caudals, while centrum length increases and decreases several times within the caudal series.) The difference in height is 1.5 mm; this corresponds to 6 vertebrae in the first group and to 9 in the second. Presumably, then, at least 6 but not more than 9 caudals intervened between the two segments preserved.

The caudal centra do not have a consistent pattern of variation in shape or length. In the first seven caudals the anterior central surface is inclined posterodorsally while the posterior surface is perpendicular to the long axis of the centrum. The remaining centra in the first group are rectangular. Centra 4 to 7 of the last block have a parallelogram outline, the dorsal margin anterior to the ventral; the other centra are rectangular. The length of the centra increases from about 15 mm for sacral 1 to about 18 mm for sacral 11. In the second group, length is approximately constant at 16 mm.

Several features are common to the first nine caudal centra. The ventral margin is markedly concave; this is accentuated by the inferiorly projecting articulation with the chevrons. Beyond caudal 9 the area of heamal arch articulation decreases and the inferior border becomes more gently concave. On the lateral surface of the centra a fossa lies below the transverse process; a ridge marks the middle of the ventral margin. The size of the fossa decreases from the first to ninth caudal and disappears at caudal 10.

Transverse processes are found on all twelve caudals of the first group and on the first twelve caudals of the second. The processes maintain the same relative position throughout, projecting from the middle of the centrum just below the neurocentral junction. The processes of the first nine caudals are horizontal and angled posteriorly; all the rest are successively smaller projections but perpendicular to the centrum.

The neural arches of the first ten caudals have spinous processes, the remaining caudals do not. In the first ten, the spine both decreases in height and inclines more posteriorly. The first seven spines are about 15 mm high while the

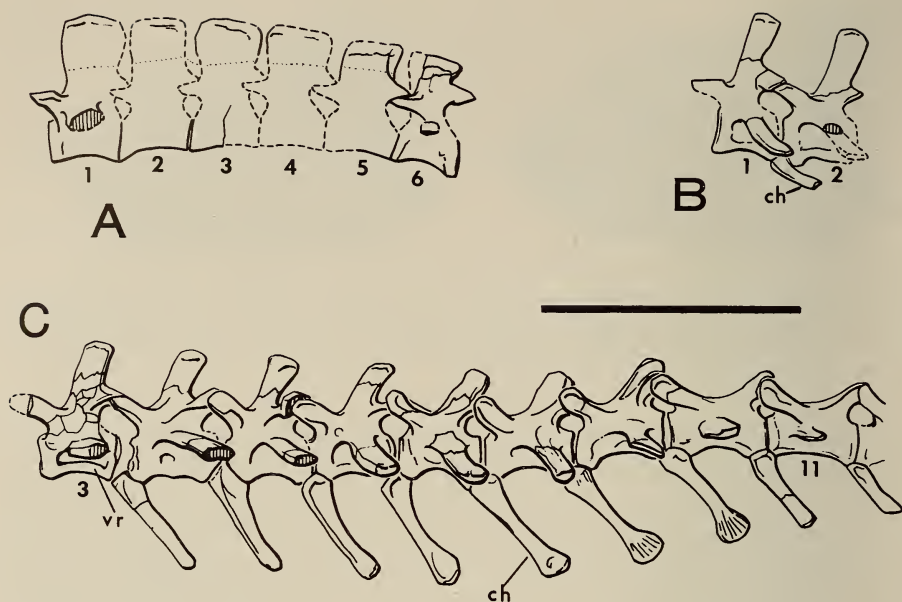


Fig. 7. *H. tucki*. A. Sacral vertebrae, left lateral view; outline of S 2-5 taken from radiograph. B. First two caudal vertebrae, from main matrix block, left lateral view. C. Caudal vertebrae 3-12, from matrix block illustrated in Figure 6, left lateral view. Scale = 5 cm.

remainder diminish rapidly in height. The inclination of the spines to the horizontal plane decreases from about  $90^\circ$  in the first sacral to about  $45^\circ$  in the tenth; in this last, the spine is almost parallel to the postzygapophyseal process. The zygapophyseal processes are set at about  $40^\circ$  to the horizontal plane in the first group of caudals; this angle decreases to about  $30^\circ$  in the second group. The transverse axis of the articular facets increases from about  $45^\circ$  relative to the horizontal plane at the sacrocaudal junction to almost  $90^\circ$  after the first six or seven caudals.

All the caudal vertebrae preserved had chevrons. The first six chevrons are expanded proximally, having relatively large articular contacts with the centra;

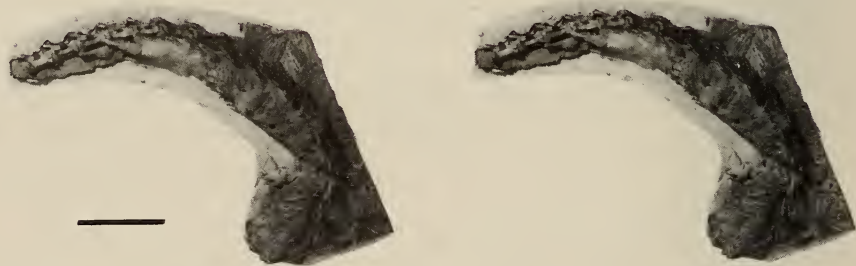


Fig. 8. *H. tucki*. Stereophotograph of second block of caudal vertebrae. Scale = 5 cm.

distally, these chevrons narrow to a small rod. From the seventh chevron of the first group to the sixth of the second, the distal end of the chevron is antero-posteriorly expanded into a knob. The length of the chevrons decreases progressively from about the ninth. The first chevron preserved on the last block is 20–21 mm long; the fifth behind that is about 18 mm long; and the last complete chevron is still 16 mm long (on the third from last vertebra). If the reduction in chevron length were a linear function, then 15–20 vertebrae would have completed the caudal series if the smallest chevron were 8–10 mm long.

### Comparisons

The total number of presacral and sacral vertebrae in *H. tucki* ( $9+12+6$ ) cannot be matched in any of the well-known ornithopods such as *Hypsilophodon* ( $9+15+6$ ), *Camptosaurus* ( $9+16+4/5$ ), or *Iguanodon* ( $11+17+6$ ). Only ceratopsians (including *Protoceratops*), *Psittacosaurus* and *Protiguanodon* have a similar sacral and pre-sacral count.

As a whole, the vertebral structure of *H. tucki* resembles that of *Hypsilophodon* most closely, though similarities to the non-ornithopods are frequent. The axis has a structure similar to that of the ornithopods *Hypsilophodon* and *Camptosaurus*, but also to that of *Stegosaurus*. In the remaining anterior cervicals, *H. tucki* and *Hypsilophodon* are quite similar. However, the deeply concave and short posterior cervical centra are not matched in *Hypsilophodon* but rather in *Protoceratops*.

The morphology of the dorsal vertebrae agrees with that of typical ornithopods such as *Hypsilophodon*, *Camptosaurus* and *Thescelosaurus* and with what is known of *Fabrosaurus*. The dorsals, however, are unlike those of hadrosaurs,

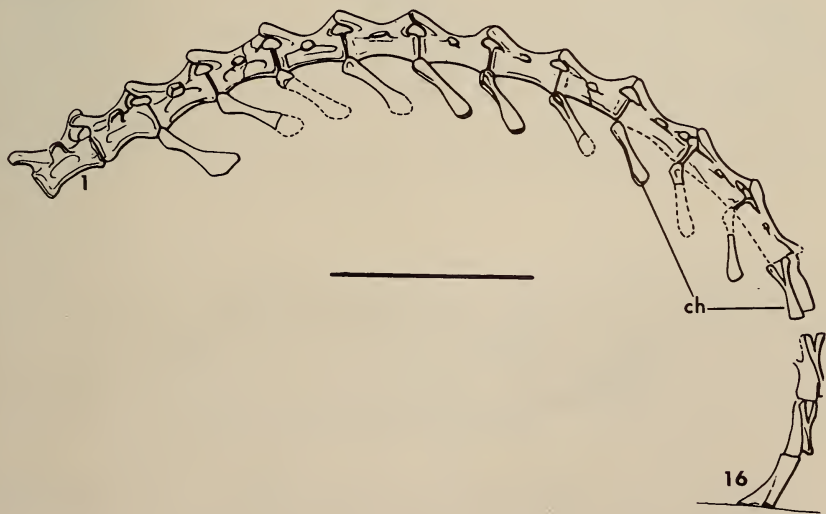


Fig. 9. *H. tucki*. Caudal vertebrae on second matrix block illustrated in Figure 8. Scale = 5 cm.



iguanodonts and some non-ornithopods (*Stegosaurus*, *Centrosaurus*) which have high and relatively narrow neural spines.

The sacral vertebrae of *H. tucki* are virtually unknown since they are buried in matrix between the ilia. The caudal vertebrae resemble those of *Hypsilophodon*, *Thescelosaurus* and *Fabrosaurus*. In *Camptosaurus*, the anterior caudals are considerably shorter but the posterior caudals much more like those of *H. tucki*. The caudals of *H. tucki* do not have the anteroposteriorly compressed centra nor the high neural spines of iguanodonts and hadrosaurs.

#### PECTORAL GIRDLE AND FORELIMB

##### *Scapula* (Figs 1, 3-4, 10D)

Both scapulae are preserved, the left presenting the external aspect, the right the inferior-external aspect. The glenoid cavity is clearly visible on the right (Figs 1, 3) as the humerus is disarticulated from the scapula, but the humeral head lies in the glenoid on the left side (Fig. 4). Both scapulae lie approximately parallel to the vertebral column, the anterior extremity somewhat more ventral than the posterior. In the reconstruction the scapula has been reoriented parallel to the vertebral column in a position comparable to that seen in well-preserved hadrosaurs (Lull & Wright 1942). An anteroventral-posterodorsal orientation of the scapular long axis would also be quite accept-

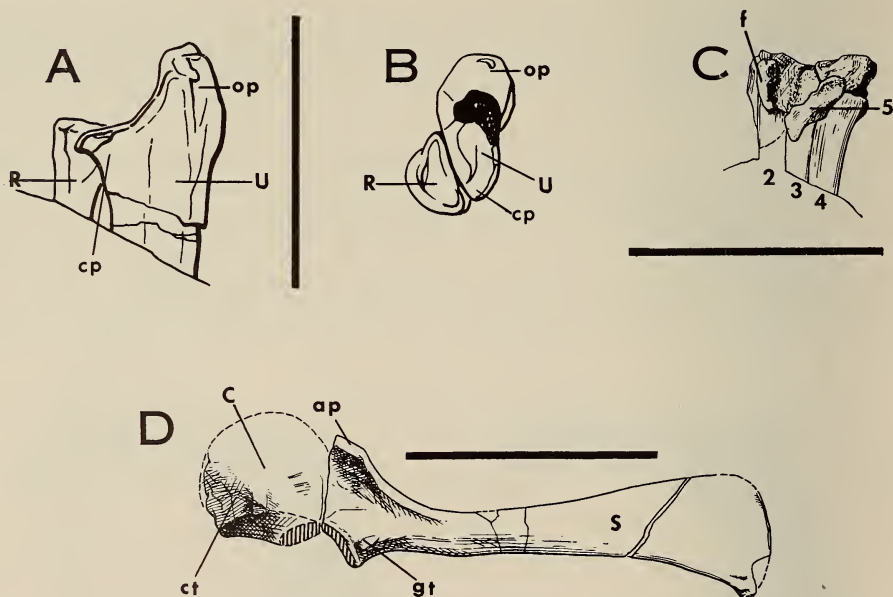


Fig. 10. *H. tucki*. A. Medial view of olecranon process, right ulna. B. Proximal articular surface, right radius and ulna. C. Right distal tarsals and proximal portion of metatarsals with reduced fifth digit, ventral view. D. Left scapula, lateral view. Scales: A-B = 2.5 cm; C-D = 5 cm.

able. In either case, the glenoid long axis should be primarily ventral in position, not posterior.

The scapula is the longest element of the shoulder girdle-forelimb complex. The caudal portion is thin and broadened into a blade; the bone at the margin here has a roughened and unfinished appearance which probably indicates a cartilaginous suprascapular extension. Along the blade-like caudal portion of the scapula, the ventral margin is strongly concave while this part of the dorsal margin is straight. Cranially, the scapula tapers considerably: it becomes sub-circular in cross-section about 20 mm proximal to the scapulocoracoid suture; it broadens out again above the glenoid but remains thick in cross-section. The scapula has only a gentle curvature to conform to the thoracic wall: the arc is 90 mm, the chord 85 mm; most of the curvature occurs just proximal to the glenoid fossa.

Along the dorsal margin above the glenoid fossa, a prominent acromial process rises about 9 mm above the scapula. The coracoid edge of the process is damaged so there is no evidence of a clavicular facet. A well-developed glenoid tubercle appears at the posterior lip of the glenoid fossa, separated from the lip by a small fissure. It probably marks the attachment of the scapular head of triceps. The glenoid itself is anteroposteriorly concave (10 mm wide) and transversely flat (5 mm thick); the cavity is 3-4 mm deep. The scapula and coracoid are firmly fused, each contributing about half of the articular area.

#### *Coracoid* (Figs 1, 3, 10D)

The left coracoid is complete except for a small area opposite the acromion and for the distal end of the plate; only the glenoid portion of the right coracoid is preserved.

The coracoid plate has flat proximal and distal halves, bent about a perpendicular to the long axis of the scapula. The proximal half is in line with the glenoid portion of the scapula, the distal half is bent medially relative to the proximal. An ovoid tubercle lies at the ventral margin approximately 10 mm distal to the glenoid fossa, at the junction of the proximal and distal coracoid halves; it is perhaps associated with the coracobrachialis or costocoracoideus muscle.

#### *Sternum* (Figs 1, 3)

What seems to be a thin sternal plate lies in matrix within the angle formed by the left humerus and scapula. Its approximate dimensions are 35 mm by 18 mm. However, the exact shape and orientation of the plate are unknown since its complete outline is not discernible: it may be either quadrangular like the sternal plates of *Hypsilophodon* (Galton 1974), or quadrangular with a handle-like process like the plates of *Iguanodon atherfieldensis* (Hooley 1925).

#### *Humerus* (Figs 1, 3-4, 11A)

Both humeri are complete but still in matrix, the left gives a posterior view and the right an anterior view so no details are lost. The shaft is only slightly

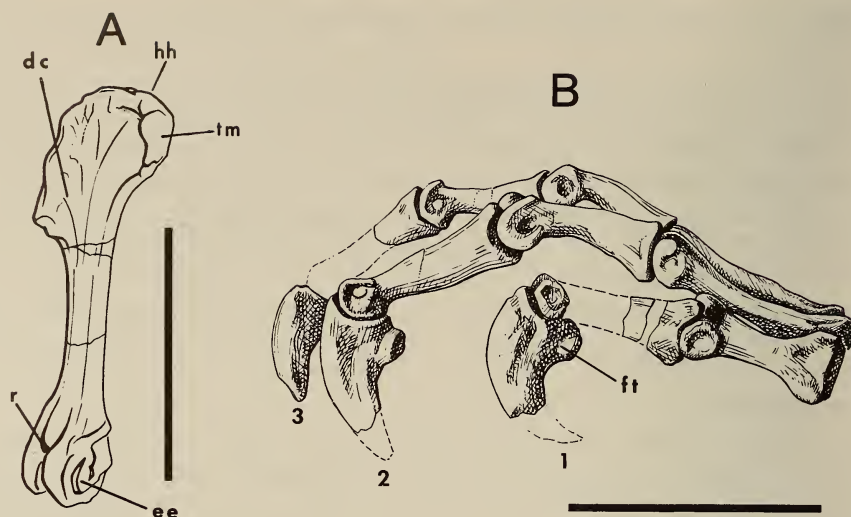


Fig. 11. *H. tucki*. A. Right humerus, dorsal view. B. Right manus, medial view.  
Scales: A = 5 cm; B = 2,5 cm.

twisted about its long axis, so the transverse axis of the proximal and of the distal articular surfaces are virtually parallel. The proximal part of the shaft with the deltopectoral crest is retroflexed relative to the distal part; the angle formed is about  $30^\circ$ .

Proximally, the humerus has a moderately well-developed articular head, bounded laterally by the superior margin of the deltopectoral crest and medially by a tuberosity lying just below the articular eminence. The head lies in the middle of the superior surface; its diameter is greater than the thickness of the proximal end of the shaft and a small fossa occurs just below the head anteriorly while a buttress of bone lies below the head posteriorly.

The deltopectoral crest occupies about 40 per cent of the lateral margin of the humerus; it ends abruptly and joins the shaft at nearly a right angle. The crest is directed anteriorly as well as laterally, so the anterior surface of the crest and shaft is concave, the posterior surface convex. The edge of the crest is thin except superiorly where it forms part of the tuberosity (for the insertion of the deltoid) and inferiorly where it is rugose and thickened for the attachment of the pectoralis muscle.

Below the deltopectoral crest the shaft is subcircular in cross-section; it becomes more rectangular distally as the supracondylar area is approached.

The medial, ulnar condyle is gently rounded both transversely and anteroposteriorly; it extends somewhat lower than the radial condyle. The radial condyle is ridge-like transversely, not rounded; a transverse section through the condyles would thus show a U-shaped ulnar condyle meeting a V-shaped radial condyle. While the anteroposterior axis of the ulnar condyle is parasagittal, the



ridge of the radial condyle is offset in an anterolateral-posteromedial direction. The radial condyle is limited above and anteriorly by a small transverse ridge, creating a shallow fossa between condyle and ridge. A small supracondylar ridge widens the humerus radially. The medial surface of the humerus just above the ulnar condyle has a strong entepicondyle sharply demarcated from the surface of the shaft. This indicates a correspondingly strong development of forearm flexor musculature. Neither condyle extends on to the dorsal surface of the shaft (Figs 1, 3); the humerus is here completely flat with no olecranon fossa though the ulna has a well-developed olecranon process. Consequently, it would be impossible for the forearm to have been fully extended on the humerus.

*Radius* (Figs 1, 3, 10B, 12-13)

Both radii are complete but still partially contained in matrix. The right radius is composed of several realigned fragments and is somewhat distorted, whereas the left is complete and undistorted. On the left radius the distal articulation is turned about  $20^{\circ}$ – $30^{\circ}$  medially relative to the proximal; a similar torsion is found in the ulna. In section, the shaft of the radius is generally subcircular; at the extremities it becomes quadrangular.

The superior articular surface (Fig. 10B) is semicircular in outline: a straight medial edge in contact with the ulna and a convex lateral margin. The fossa for the radial condyle of the humerus is an elongated shallow sulcus which matches the ridge-like nature of the condyle. Such an arrangement would stabilize the radiohumeral articulation and limit rotation of the radius. The posterior margin of the superior articular surface is raised and extended

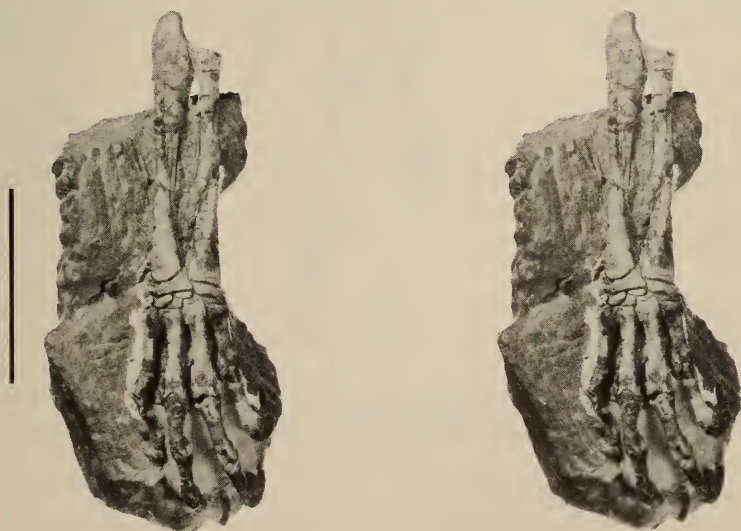


Fig. 12. *H. tucki*. Stereophotograph of right radius, ulna, carpus and manus, dorsal view.  
Scale = 5 cm.

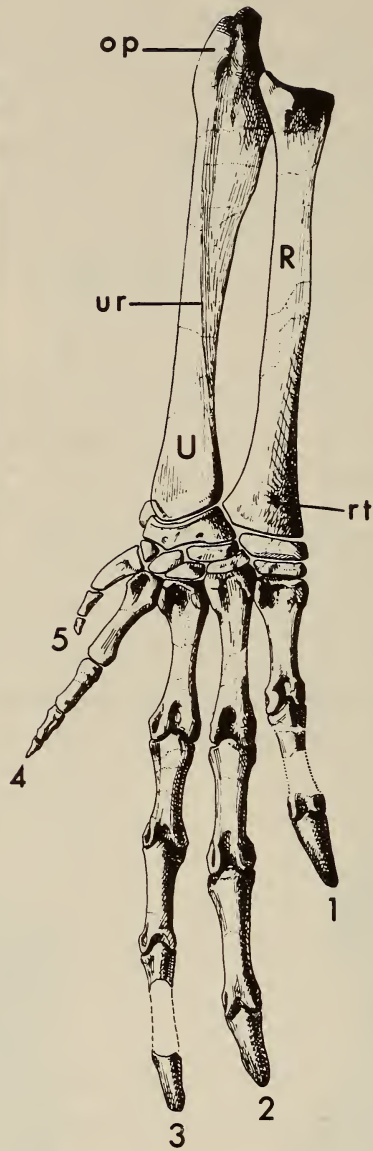


Fig. 13. *H. tucki*. Right radius, ulna, carpus and manus, dorsal view. Scale = 5 cm.

posteriorly (Fig. 12); the articular surface is thus lengthened and inclined anteroinferiorly. Distally, a small rounded tubercle lies on the dorsal surface of the shaft, 5 mm above the distal end (Fig. 13); this may be associated with an insertion of the extensor carpi radialis muscle. Distally, the shaft is expanded toward the ulnar side; here it makes an oblique contact with the ulnare. The inferior articular surface is planar, in contact with the radiale.

#### *Ulna* (Figs 1, 10A, 10B, 12–13)

Both ulnae are preserved, in articulation proximally and distally, but not freed from matrix. The left ulna presents a dorsolateral view, the right a dorso-medial view.

Proximally, the ulna has a pronounced olecranon process which rises about 10 mm above the coronoid process; the coronoid process itself projects anteriorly as an almost horizontal shelf. The olecranon part of the articular surface is wider than the coronoid part. The posterior surface of the olecranon bears a rugose, uplifted area of bone for the attachment of the triceps tendon. The radial side of the proximal ulna is convex; a small tubercle lies on this side of the olecranon process, above the coronoid (Fig. 12). The medial surface of the proximal ulna is marked by the jutting ridge for the triceps attachment and by the overhanging ridge of the articular surface; these ridges give the proximal ulna a concave appearance. The ulnar shaft narrows below the coronoid process but widens gradually towards the distal end. A long, low ridge is found on the dorsal part of the shaft beginning below the area of triceps attachment (ur, Fig. 13); it continues to the distal third of the shaft and then terminates. The distal articular surface is transversely convex, fitting into the concave proximal surface of the ulnare. Both ulna and ulnare are in contact with the pisiform laterally.

#### *Carpus* (Figs 1, 12–15)

Both left and right carpi are complete and in virtually undistorted articulation with the forelimb and metacarpus of each side. Consequently, the relative position of the carpal elements is certain; this is important since the arrangement of the proximal row of carpals differs from that known in all other ornithischian groups.

The carpus is composed of nine ossified elements, arranged in a proximal and distal row with one element sandwiched centrally between these rows. The proximal row contains the radiale, ulnare and pisiform; the distal row contains one carpal for each of the five metacarpals; finally, one carpal lies beneath the medial part of the ulnare, above distal carpal 2 and the medial part of distal carpal 3. This arrangement contrasts sharply with the carpal construction of known ornithischians. Properly speaking, the bone intervening between the two rows of carpals does not correspond to an *os intermedium*; rather, it corresponds in position to an *os centrale*.

Comparisons with other ornithischians are hindered because so few com-





Fig. 14. *H. tucki*. Stereophotograph of right carpal region, dorsal view. Scale = 5 cm.

plete carpi exist; however, the complete carpus of *Camptosaurus dispar* (Gilmore 1909) does not contain an os centrale, only an os intermedium. An os centrale does exist in the carpus of the alligator (but along with an os intermedium) so it would not be unusual to find its retention in an early ornithischian archosaur. A number of possibilities exist with respect to the fate of the os intermedium in *Heterodontosaurus*, but it is impossible to choose among them: (i) the os intermedium has been lost in the *Heterodontosaurus* lineage; (ii) the os intermedium has fused with the ulnare, as in *Stegosaurus* (Gilmore 1914); (iii) the os intermedium has fused with the radiale; (iv) the os intermedium has become displaced inferiorly by the growth of the radiale and/or ulnare, to occupy the position of an os centrale. The phylogenetic history of the carpus in *Heterodontosaurus* thus remains unknown for the present.

The radiale is a flat, plate-like bone, articulating with the entire distal surface of the radius; it is transversely elongated to match the distal, expanded shaft of the radius. The ulnare, proximodistally thicker than the radiale, contacts the radiale on the inferior half of its medial margin while the superior half of the medial margin is in contact with the distal end of the radial shaft. As noted above, the superior surface of the ulnare is transversely concave to accept the rounded end of the ulnar shaft; distally, the ulnare has a flat articular surface. The lateral surface of the ulnare has two facets, the inferolateral for distal carpal 5, the superolateral for the pisiform. The pisiform is a cuboidal element in contact with both ulnare and ulna. The intervening bony element in the carpus is biplanar, in contact proximally only with the ulnare, but with distal carpals 2, 3 and 4 below.

Distal carpals 1 and 2 are both thin, biplanar elements, sandwiched between the carpals above and the metacarpals below. Distal carpal 3 is proximodistally thicker than 1 and 2, rectangular medially, but the lateral margin is diagonal. The diagonal margin permits distal carpal 4 to intervene between the ulnare

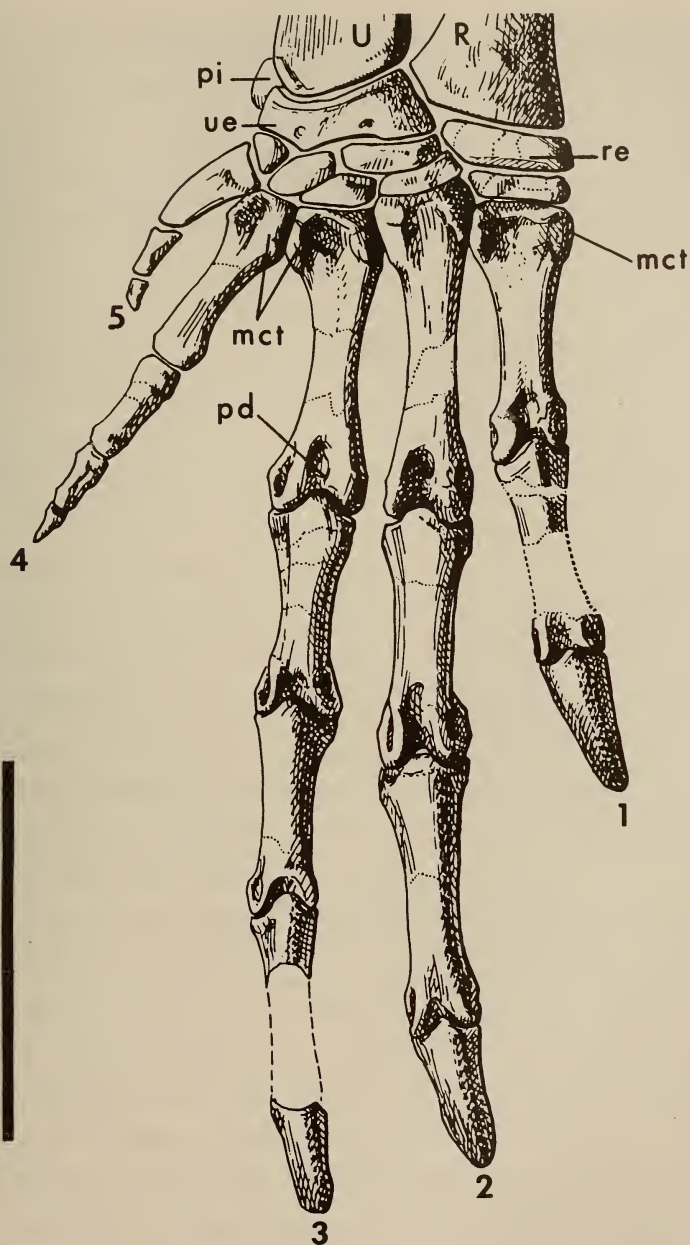


Fig. 15. *H. tucki*. Detail of right carpus and manus. Scale = 2,5 cm.

above and distal carpal 3 below. The inferolateral surface of distal carpal 4 is offset in such a way that digit 4 is highly abducted with respect to digits 1-3. Distal carpal 5 is cuboidal, articulating with the inferior facet of the ulnare's lateral surface. The inferior facet of the ulnare faces laterally as well as inferiorly; consequently, the fifth digit is abducted and lies parallel to digit 4. The orientation of the carpal bones results unquestionably in a manus with the 3 medial digits parallel to each other and digits 4 and 5 abducted with respect to the first three but parallel to each other.

*Manus* (Figs 1, 11B, 12-13, 15)

Both left and right manus are virtually complete. The left lacks only the distal portions of the metacarpal and phalanges of digit 2. The right lacks the distal portion of phalanx 1, digit 1, and of phalanx 3, digit 3; none of the right fifth digit is visible (though the proximal part may still be in matrix, the distal portion is certainly missing). Most of each manus is still embedded in matrix, so only the dorsal surface of the digits is usually visible. The phalangeal formula is 2-3-4-3-2.

The base of metacarpal 1 is transversely expanded and dorsoventrally flattened, making it a thin rectangle in section (metacarpal 1 is seen in oblique view in Fig. 11B). The metacarpal narrows below the base so the medial and lateral margins are both concave. A tubercle, about 3 mm long, lies at the uppermost medial margin of the metacarpal base, in the position of attachment of the supinator manus muscle of modern reptiles (Fig. 15). On the lateral half of the metacarpal base the articular facet extends a short distance on to the dorsal surface of the metacarpal, allowing extension of the metacarpal on the distal carpal. The metacarpal bears another tubercle at the uppermost lateral margin of the dorsal surface, in contact with a similar protuberance at the base of metacarpal 2. The heads of metacarpals 2-4 each bear such a tubercle at both the uppermost medial and lateral dorsal margin. These tubercles correspond to the attachments of the humerodorsalis muscle of reptiles and amphibians. The condition of *Heterodontosaurus* indicates at least seven slips of attachment, not a reduced number as seen in *Varanus*, *Sphenodon* and *Alligator* (Haines 1939).

Distally, each of the first three metacarpals bears a deep pit on the dorsal surface just proximal to the articular head. This receives a well-developed dorsal process of the phalangeal base. The distal articular surface of the first three metacarpals continues on to the dorsal surface, just distal to the pit. This prolongation of the articular surface permits hyperextension of the proximal phalanges on the metacarpal heads of digits 1-3. This is important during quadrupedal progression (plantigrade) when the forelimb is weight-bearing, and supports the hypothesis that *Heterodontosaurus* was capable of quadrupedal locomotion.

The distal articular surface of metacarpal 1 is complex and asymmetric (Figs 11B, 15). The outline of the medial condyle is subelliptical, its long axis proximodistal, that is, oriented on the long axis of the metacarpal. The lateral



condyle is also subelliptical, but its long axis is perpendicular to the medial condyle, that is, directed dorsoventrally. Thus, the lateral condyle rises above the dorsal surface of the metacarpal shaft while the medial condyle is flush with this surface. In addition, the pits for the collateral ligaments have relatively different positions due to the difference in condyle orientation. The pit for the medial collateral ligament lies midway between the dorsal and ventral margins; the pit for the lateral collateral ligament lies just at or above the dorsal surface of the metacarpal. Dorsally, the intercondylar groove lies medial to the midline of the joint, the lateral condyle being wider than the medial. The metacarpal is also asymmetric in length: the lateral edge is longer than the medial edge. This produces an oblique transverse axis of rotation which has two effects: first, the phalanges of digit 1 would be medially offset (though the metacarpal is not) in extension; second, the phalanges would be laterally offset during rotation around the oblique axis of the joint.

The bases of metacarpals 2-5 differ from that of metacarpal 1 in being almost square in section, not dorsoventrally flattened. These metacarpals have an almost square dorsal outline resulting from the planar articulations with the distal carpals and with the adjacent metacarpals. The carpometacarpal articulation of metacarpal 2 carries on to the dorsal surface for a short distance; this would permit some extension of the metacarpal on the carpus. In metacarpal 3, the articulation with the distal carpal does not extend on to the dorsal metacarpal surface; the boundary between the carpal and dorsal surfaces is a sharp ridge, not a smooth, curved transition as in metacarpals 1 and 2.

The metacarpophalangeal joint of digit 2 is symmetrical, the two condyles being of equal size. Flexion-extension here would result only in movement along the long axis of the metacarpal. The metacarpophalangeal joint of digit 3 is smaller but also seems to be symmetrical (the view of the medial surface is limited since digit 3 lies very close to digit 2).

Digits 4 and 5 are extremely reduced and apparently non-functional. The total length of digit 4 hardly exceeds the length of metacarpal 3. However, the base of metacarpal 4 is almost as large as the bases of metacarpals 2 and 3. This may be correlated with the still large attachment for the humerodorsalis on metacarpal 4. The head of metacarpal 4 is quite small; it is covered with a black concretion which obscures the details of the metacarpophalangeal joint. The base of metacarpal 5 is convex dorsally without any tubercles, indicating the humerodorsalis had lost all attachment to the fifth digit.

Atrophy of digits 4 and 5 occurs in both known Late Triassic ornithischians, *Heterodontosaurus* and *Fabrosaurus*, and in almost all other Jurassic-Cretaceous ornithischians as well. Consequently, the reduction of the lateral digits occurred very early in the phylogenetic history of the group or was characteristic of the ancestral group which gave rise to ornithischians. Gilmore's interpretation, for example, that digit 5 of *Camptosaurus* 'was becoming atrophied' (1909: 256) is thus not accurate. The digit had already become reduced in previous forms and was merely the expression of an ancestral trait.

Apart from the unguals, the phalanges of the first 3 digits can be placed in 2 categories. The simpler has a symmetric articular facet both proximally and distally; these are the penultimate phalanges of digits 1-3. The base of each has a well-developed median dorsal and median ventral process. Distally, the outline of the articular facet for the ungual phalanx is not uniformly rounded but is somewhat flattened dorsally. The articular surface extends farther on to the ventral than the dorsal aspect of the phalanx. The pits for the collateral ligaments are found near the dorsal surface of the phalanx on both lateral and medial sides.

In the other category of nonungual phalanges are those which intervene between the metacarpal and the penultimate phalanx: phalanx 1 of digit 2, and phalanges 1 and 2 of digit 3. These phalanges have a symmetric base proximally but an asymmetric head distally (Fig. 12). The asymmetry involves, firstly, a torsion of the head relative to the base which turns the ventral surface of the digit somewhat medially. Secondly, the length of the phalanx along the medial margin is a little less than along the lateral margin: this directs the longitudinal axis of the succeeding digit medially. Thirdly, the condyles themselves are asymmetric: the medial condyle is larger than the lateral, and the trochlear surface of the medial condyle is not as steep as that of the lateral condyle. The outline of the medial condyle is a half ellipse, its long axis pointed ventrally about  $45^\circ$  to the long axis of the phalanx; the outline of the lateral condyle is also a half ellipse, but its long axis parallels that of the phalanx (see the head of phalanx 1, digit 2, Fig. 11B). The depressions for the collateral ligaments are found near the ventral margin medially but near the dorsal border laterally. The transverse axis of the joint is thus dorsolateral-ventromedial, with the dorso-lateral edge being slightly distal to the ventromedial. Rotation about this axis would produce a medial-to-lateral movement during flexion like that of digit 1.

The first three ungual phalanges are large, lateromedially compressed claws. The proximal ventral surface bears a protruding flexor tubercle for the attachment of the long flexor tendons (Fig. 11B). A comparable development of flexor tubercles is found nowhere else in the Ornithischia. The lateral and the medial surface of the unguals has an irregular depression midway between the dorsal and ventral margins about 3 mm distal to the articular surface. This probably marks the distal attachment of the collateral ligaments.

The phalanges of digits 4 and 5 are quite diminutive; those of digit 4 have recognizable articulations permitting flexion-extension, but are very simplified. The articular surfaces are dorsoventrally rounded; the phalangeal heads have a single uniform articular surface without clearly defined medial and lateral condyles. The terminal phalanx of digit 4 is dorsoventrally flattened, triangular in outline. The proximal phalanx of digit 5 is much too small for details to have been retained during preparation. It has a concave proximal and convex distal articular surface. A small fragment of bone distal to the phalanx may be part or all of the next and presumably terminal phalanx: it is only about 1,5 mm long.

### Comparisons

The scapular morphology of *H. tucki* approaches that of conservative ornithopods (*Hypsilophodon*, *Thescelosaurus*, and *Camptosaurus*) more than that of other ornithopods (*Anatosaurus* or *Iguanodon*). It differs from that of ceratopsians, stegosaurs and ankylosaurs which have a more nearly uniform width of the scapular blade. However, the non-ornithopods are no more different from *H. tucki* than *Anatosaurus* and *Iguanodon*.

The humerus of *H. tucki* is relatively more robust than that of conservative ornithopods and *Fabrosaurus*. Most of the differences are probably related to the forelimb capabilities of *H. tucki*, both quadrupedal and prehensile. The relatively larger deltopectoral crest and the entepicondyle are more reminiscent of the large ornithischian quadrupeds such as *Stegosaurus* and *Triceratops*. However, hadrosaurs have a deltopectoral crest larger than that of *H. tucki*. In one feature, the humerus of *H. tucki* seems unlike that of any other ornithischian: the lack of a posterior intercondylar groove or depression between the radial and ulnar condyles. This would have severely limited elbow extension; consequently, *H. tucki* may have assumed a semi-sprawling posture with the forelimbs.

In *H. tucki*, the extremities of the radius are expanded relative to the shaft, somewhat more than they are in the radii of *Hypsilophodon*, *Camptosaurus*, *Thescelosaurus*, and *Anatosaurus*, but very similar to those of the radius of *Iguanodon*. In fact, as a whole the forearm of *Iguanodon* is more similar to that of *H. tucki* than are the forearms of other ornithischians. The radii of the large quadrupedal forms are variable: those of ceratopsians are but little expanded at the extremities but that of *Stegosaurus* is much more so. The ulna of *H. tucki* has a relatively well-developed olecranon process, a feature usually found in the heavy quadrupedal ornithischians; however, the ulna of the small *Microceratops* also has an olecranon process. Only *Iguanodon* among the ornithopods seems to have a comparably developed process.

Because the carpus is incomplete in so many ornithischians, the precise orientation of the metacarpals remains uncertain in these cases. Digits 4 and 5 are clearly deviated to the ulnar side in *H. tucki*; however, in *Fabrosaurus* and *Hypsilophodon* the manus was reconstructed with only digit 5 abducted. In the latter two genera, however, digit 4 may also have been abducted since the carpals, which would have determined digit orientation, are missing.

The only previously published illustration of the carpus and manus of *H. tucki* (Bakker & Galton 1974, fig. 1H) is completely inaccurate. On the basis of that inaccurate reconstruction, the authors argued that the hand of *H. tucki* was identical to that of Triassic saurischians and was most likely inherited from Triassic saurischians. In fact, the properly reconstructed hand of *H. tucki* is more reminiscent of that of thecodontians than of early saurischians.

The phalangeal formula in *Heterodontosaurus* is 2-3-4-3-2. This agrees with that of *Hypsilophodon* (according to Gilmore 1915), *Thescelosaurus* and the ceratopsians; it differs from that of *Camptosaurus* (2-3-3-3-2), *Trachodon* (0-3-3-3-3) and *Iguanodon* (1-3-3-3-4). *Trachodon* and *Iguanodon* are



anomalous in the number of phalanges in the fifth digit; it seems unlikely that such a phalangeal formula could have been derived from that of *H. tucki* since it would require an increase in the number of phalanges in a non-functional digit and a change of this digit to a functional role in the animal's behaviour. By inference, then, *Trachodon* and *Iguanodon* could not be derived from any genus having only two phalanges in digit 5; thus, they represent a deviation in ornithischian phylogeny about the origin of which we have no information.

#### PELVIC GIRDLE AND HIND LIMB

##### *Pelvis* (Figs 1, 3-4, 16-18A)

Both pelves are preserved but the left is somewhat damaged. The left ilium has been displaced ventrally while the right has been displaced dorsally. The ilia are also lateromedially compressed; this has compacted the sacral ribs and transverse processes and considerably narrowed the interacetabular width of the pelvis. The left anterior iliac process is broken and shifted ventrally; this creates a greater convexity than the ilium actually had. The left prepubic process has been completely crushed, its original form destroyed; fortunately, the right prepubic process is well preserved. A fracture through the left ilio-ischial suture distorts this region, but the right side is undamaged here. The fracture separating the main matrix block from the first caudal vertebrae block (Fig. 1) also divides the postpubes and ischia in midlength but no bone has been lost and the shafts are complete.

##### *Ilium*

The ilium of *H. tucki* has a shallow, elongated anterior and posterior process. The anterior process extends about 45 mm anterior to the pubic peduncle; this constitutes 44 per cent of total iliac length. Anteriorly the process veers away from the vertebral column and ends opposite the last dorsal vertebra. A small ventral flange or convexity gives a bulbous appearance to the last 10 mm of the process. The first three sacral vertebrae join the slender anterior process; furthermore, the rib of the last dorsal vertebra was probably fused to the tip of the process. This rib is short (19 mm) and could not have extended beyond the ilium. The posterior iliac process is shorter than the anterior (28 mm from the ischial peduncle) but equally shallow; it ends in a small, rounded expansion. The brevis shelf is horizontal but shallow, extending 4-6 mm medially from the ventral margin of the process to join the last sacral vertebra.

The acetabulum of *H. tucki* is 22 mm high and 20 mm long at its base. The pubic peduncle is relatively long compared to other ornithischians (18 mm from the notch between the anterior process and peduncle to the ilio-pubic suture). The peduncle is almost vertical, inclined only about 20° anterior to a perpendicular from the long axis of the ilium. The anterior and posteroventral acetabular margins are raised into a sharp ridge while the dorsal and ventral acetabular margins are rounded and flush with the surface of the ilium and puboischium.

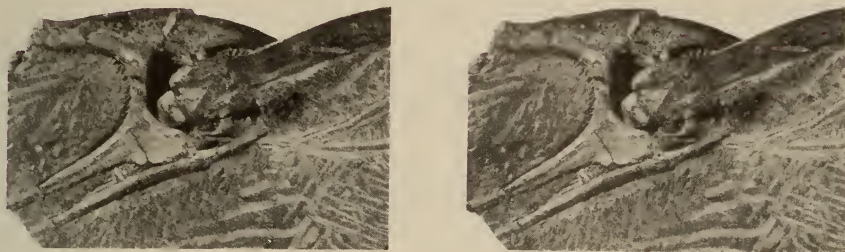


Fig. 16. *H. tucki*. Stereophotograph of right pelvis, lateral view. Scale = 5 cm.

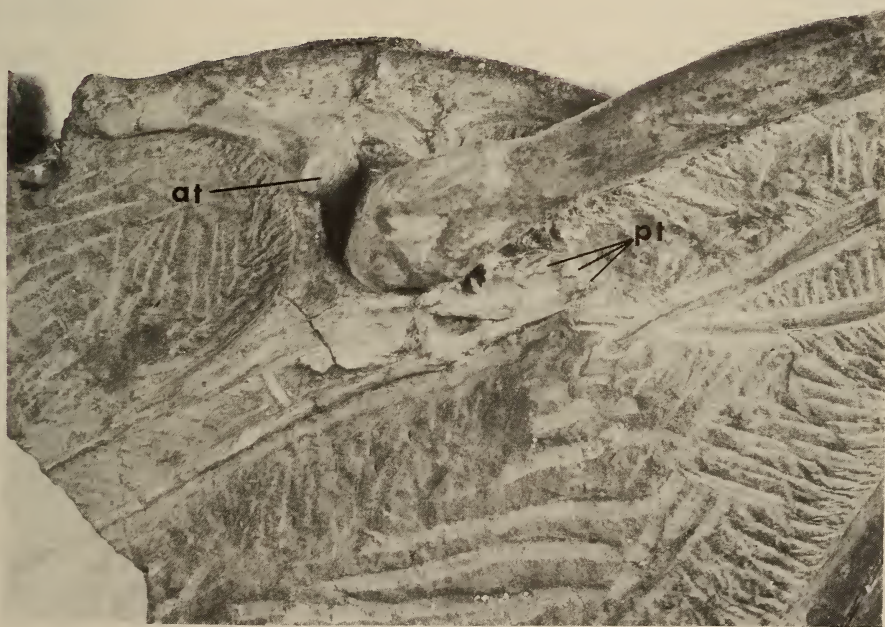


Fig. 17. *H. tucki*. Detail of right pelvic region. Scale = 5 cm.

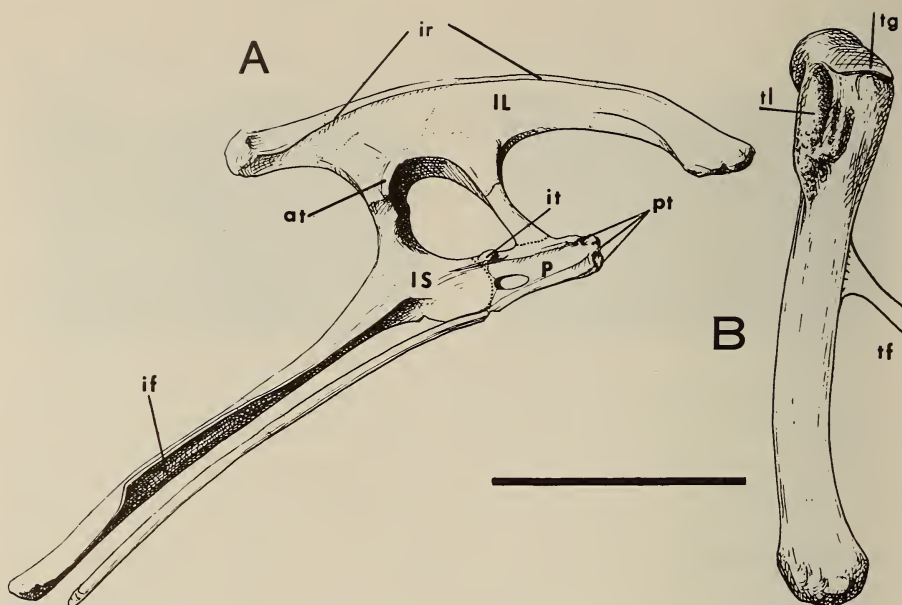


Fig. 18. *H. tucki*. A. Right pelvis, lateral view. B. Left femur, lateral view. Scale = 5 cm.

The single most important feature of the acetabulum is the expanded articular surface at the posterodorsal corner. Here the ischiadic peduncle of the ilium flares out, creating an horizontal articular shelf and buttress against which the femoral head would have rested. The ventral surface of this shelf is a continuation of the acetabulum and would have borne articular cartilage during life. The ilio-ischial suture lies below this buttress and is separate from it. Structurally, this articular buttress closely resembles the antitrochanter of birds (completely different from the 'antitrochanter' of dinosaurs). Very strong ligaments connect the iliac antitrochanter and the femoral greater trochanter in birds. This system resists the collapse of the body on the femur when the body is supported by only one leg. Unquestionably, the structural similarity to the avian acetabulum argues that some similar mechanical system in the pelvis and hind limb of *H. tucki* prevented excessive pelvic tilt when weight was borne by a single hind limb.

The dorsal margin of the ilium is slightly convex; its arc is 101 mm while the chord (that is, maximum iliac length) is 96,7 mm. A ridge for muscle attachment runs from the tip of the anterior to the tip of the posterior process: beginning on the ventral flange of the anterior process, it passes obliquely upwards to the dorsal margin of the ilium, 20 mm behind the tip of the anterior process; the very last 15 mm of the ridge descends from the dorsal rim to the middle of the lateral surface of the posterior iliac process. In Romer's reconstruction of the hind limb musculature of *Thescelosaurus* (1927a) this ridge marks the attachment of the ilio-tibialis and ilio-fibularis muscles. The ilio-tibialis 1



would be above the ridge on the anterior iliac process; the ilio-tibialis 2 would be attached above the ridge along the dorsal margin; the ilio-fibularis would lie below the ridge on the posterior process; the ilio-caudalis would lie above the ilio-fibularis and the ridge. A small tubercle situated ventrally on the tip of the posterior process may indicate the attachment of flexor tibialis externus (ilioflexorius). The coccygeofemoralis brevis is, of course, attached to the small, horizontal brevis shelf.

Below the ilio-tibialis ridge, the lateral iliac surface presents no muscular ridges. The cortical bone has been fractured in many places; on the right, overlapping fractures simulate a dividing ridge between muscle masses, but it is purely artificial. This means that no demarcation can be found between the supposed attachments of ilio-femoralis externus and ilio-trochantericus 1. Romer (1927a: 264) could not find any limiting ridges either and so based his reconstruction of *Thescelosaurus* on the position of the antitrochanter of hadrosaurs and, probably, on the position of these two muscles in birds. Recently, Walker (1977) argued that the iliotrochanterici should be considered part of the ilio-femoralis externus and should not be reconstructed as a separate muscle. Thus, he proposed a single deep dorsal muscle mass, the ilio-femoralis externus, originating below the ilio-tibialis ridge and inserting on the lesser trochanter. The confusion develops because the embryonic origin of the ilio-trochanterici is uncertain (Romer 1927b, 1942). Walker's argument is weak because he drew his analogy with the development of the thigh musculature of *Lacerta* (described by Romer 1942); however, the avian condition is certainly a better model for ornithischian musculature than the lacertilian.

### *Ischium*

The ischium of *H. tucki* has a long, columnar iliac peduncle and a flat, deep pubic peduncle. The iliac peduncle is 15 mm high and 5 mm in diameter; the pubic peduncle is 9 mm deep. The ischial rods are straight and do not seem to be fused together. The rod bears a robust, laterally projecting ridge (if, Fig. 18A) beginning about 35 mm behind the acetabular border and continuing to the end of the rod; a similar feature is present on the ischium of *Protiguanodon*. In mid-length, the ridge becomes drawn out laterally into a shelf which may have provided attachment for the flexor tibialis internus and probably the ischio-trochantericus. Romer noted (1927a: 248) that the flexor tibialis internus probably arose from the dorsal margin of the ischial rod half-way along its length; since this position corresponds with that of the shelf in *H. tucki*, the flexor tibialis internus may have attached here. A short, roughened line on the proximal part of the ischial shaft and pubic peduncle may mark the adductor musculature; this line lies below and anterior to the above ridge. The area below the major ridge on the ischial rod was probably occupied by the obturator internus (pubo-ischio-femoralis externus). The ischial rod of *H. tucki* does not have an obturator process. However, the only real criterion for classification within the Ornithopoda seems to have been a bipedal form of locomotion; it is a

functional category in which several independent phylogenetic lineages may be included.

### *Pubis*

The pubis of *H. tucki* is the first which shows the configuration of the early ornithischian prepubis. The prepubic process is short and deep, 11 mm long from the anterior edge of the pubic peduncle of the ilium, and about 8 mm deep. The postpubis is thin and fragile, as long as the ischial rod, lying parallel to and about 5–8 mm below it. The postpubis seems devoid of muscle markings except on the internal surface opposite the shelf-like process on the ischium. Here a small, longitudinal, roughened area may indicate the obturator internus muscle. The obturator foramen ventral to the acetabulum is closed posteriorly by the pubis itself, not by the ischium. A tubercle lies above the obturator foramen on the ventral margin of the acetabulum; no corresponding tubercle exists in the alligator but in *Struthio* (Gadow, in Gregory & Camp 1918, pl. 46) a tubercle in this position marks the attachment of the mm accessorii.

While the postpubis has few signs of muscle attachments, the prepubis has several prominent tubercles and ridges which indicate its importance for muscle attachment (Figs 16–18A). A small, smooth ridge parallels the dorsal margin of the prepubis and terminates at the anterosuperior edge in a small but distinct tubercle. Another tubercle below the former lies on the anterior edge of the prepubis surrounded dorsally and ventrally by small damaged and pitted areas. These two tubercles have rounded, finished edges showing that they were not part of a single continuous ridge on the anterior margin of the prepubis. The anteroventral corner bears another, smaller, tubercle; its original extent is indeterminate because this corner is also slightly pitted and damaged. A short ridge runs along the ventral margin of the prepubis but ends below the obturator foramen and does not continue on to the postpubis.

The question of which muscles attached to the prepubis has never been resolved. Romer (1927a) thought only the abdominal musculature would have attached here. Galton (1969) disagreed and, in addition to the abdominal musculature, placed the ambiens, pubo-tibialis and part of the pubo-ischio-femoralis internus (ilio-femoralis internus of birds) on the prepubis. The muscle markings of *H. tucki* cannot themselves solve this problem, but they show that Romer was wrong, at least in the case of *H. tucki*, in placing only the abdominal musculature here. Romer rejected the idea of other muscles attaching to the prepubis because the most primitive ornithischians known, the hypsilophodontids, had a long, thin prepubis; this would have placed some muscle origins too far forward to have provided a firm support for muscular contractions. These are not problems in *H. tucki* because the prepubis is short and sturdy. The ambiens and a head of pubo-ischio-femoralis internus could each have originated from one of the tubercles. However, the pubo-tibialis is an unlikely muscle to attach to the prepubis; its absence in both birds and crocodiles certainly means it had a low probability of appearing in ornithischians. More likely, a

further head of pubo-ischio-femoralis internus or an embryonic derivative of the same muscle mass, the ilio-trochanterici, also originated from the prepubis.

The avian model for prepubic musculature may be sounder than realized before. The prepubic process of the earliest known ornithischians was clearly short and stout, not long and thin. This is precisely the shape of the pectineal process in the embryo chick. Only during later embryonic development does the pectineal process become relatively and absolutely small. This occurs as the pectineal process stops growing and becomes incorporated into the other pelvic cartilages during their expansion (Johnson 1883). But originally, the pectineal process of the chick has the same relative size, shape and position as the prepubis of *H. tucki* (though the pectineal process is an iliac, not a pubic, derivative in birds). Because of this similarity the musculature of the avian pre-acetabular area could be used as a model for the ornithischian prepubic musculature.

#### *Femur* (Figs 1, 3-4, 18B, 19)

Both femora are complete but each has been damaged. The left is fractured somewhat proximal to the condyles; the proximal portion is on the main matrix block while the distal end is on a separate block with the tibia-fibula. The fourth trochanter is on a third block, that containing the first group of caudal vertebrae. The right femur is in articulation with tibia-fibula and pelvis, but is only partially exposed from the matrix. The right fourth trochanter is still buried in matrix except for its lateral edge. The proximal tips of the right greater and lesser trochanters have not been preserved.

The femur of *H. tucki* differs from that of ornithopods in that the lesser trochanter is not separated by a cleft from the femoral shaft. Instead, the lesser trochanter is a protuberant crest at the anterolateral femoral margin (Figs 16-18B). It begins just below the level of the femoral head and is about 20 mm long. The anteromedial surface is smooth and continuous with preaxial surface. The lateral surface, however, is extremely rough and irregular. Romer (1927a: 256) remarked that the lesser trochanter was independent of the greater in the more primitive ornithischians, since only some stegosaurs and the ankylosaurs did not have independent lesser trochanters. But this is not a question simply of primitiveness. As with the obturator process, both conditions of the lesser trochanter appear in the Upper Triassic of South Africa: *H. tucki* with the lesser trochanter joined to the femoral shaft, *Fabrosaurus* with a cleft between lesser trochanter and shaft. The two configurations may thus be independent of each other, representing two different ornithischian lineages.

Neither does the greater trochanter of *H. tucki* correspond to Romer's (1927a: 254) description of the primitive form. Ordinarily, a depression separates the femoral head from the greater trochanter. But in *H. tucki* both head and greater trochanter are on the same level; in fact, the greater trochanter is distinguished from the lateral femoral surface only by a low, horizontal ridge and an uplifted area above this for tendinous attachment.

The 4th trochanter is a pendant, rod-like process, 14 mm long; it makes an





Fig. 19. *H. tucki*. Stereophotograph of matrix block containing left distal femur and tibiotarsus. Note transversely oblique proximal tibial surface. Scale = 5 cm.

approximate  $45^\circ$  angle with the shaft. Two parallel ridges run along the lateral surface of the trochanter, creating a shallow sulcus between them; the sulcus presumably marks the attachment of coccygeo(caudi)-femoralis brevis. The medial surface of the femur is not visible at the trochanter so the insertion of caudi-femoralis longus cannot be checked.

Distally, the lateral femoral condyle is the smaller, about 18 mm long, the inner condyle much larger, 24 mm long (Figs 1, 19). Anteriorly and posteriorly, the condyles are not separated by an intercondylar groove. While *Fabrosaurus* does not have an anterior groove it does have a posterior intercondylar groove. Presumably, the posterior groove is absent in *H. tucki* because the outer condyle is so poorly developed posteriorly.

The transverse axis of the distal femoral articular surface is oblique, that is, the transverse axis is inclined, the lateral edge lower than the medial. However, the superior articular surface of the tibia-fibula is horizontal. Consequently, the femur must be abducted relative to the pelvis to keep the articulation with the tibia-fibula horizontal. A perfectly parasagittal orientation of the femur, often depicted in reconstructions of bipedal dinosaurs, was impossible in *H. tucki*. Furthermore, the femoral head must have rested against the articular surface of the antitrochanter-like buttress of the ilium to support the body weight. Thus, the femur, in addition to being abducted, would be protracted, so the long axis of the femur passed through the antitrochanter-like articular area. The femur could not have been held vertically for several reasons: firstly, the interace-

tabular width of *H. tucki* was not great, consequently, vertically oriented femora would have impinged on the abdomen; secondly, the inferior femoral articular surface is oblique relative to the long axis of the shaft, so a horizontal, stable articular surface could be obtained only with the femur abducted; thirdly, even if a wedge-shaped articular cartilage intervened between tibia and femur to produce a vertical limb, loading would produce a sliding of the femur relative to the tibia and thus an unstable knee joint. Thus, the only possible position of the femur in *H. tucki* is abducted and protracted.

*Tibia and fibula* (Figs 1, 3-4, 19-20A)

Both tibiae are complete, but the left is fractured so that the fibula and calcaneum are displaced ventrally. The cortical bone is eroded in many places, particularly on the distal surface of the right tibia.

Structurally, the tibia-fibula of *H. tucki* is a tibiotarsus: the astragalus and calcaneum are completely fused with the tibia and fibula and the fibula is fused distally with the tibia. No sutures remain distally between the tibia-fibula and the proximal tarsals. Fusion occurred in stegosaurs and certaopsians but not in the known ornithopods.

Proximally, the inner tibial condyle is lateromedially compressed, only 7 mm wide, but anteroposteriorly expanded, 31 mm long. The great length is partially due to the cnemial crest on the medial side of the tibial head. The outer condyle is small, 12 mm long. It sits on a strong lateral buttress (hidden by the displaced fibula in Figs 1, 19-20; see Fig. 4) which extends 40 mm down the tibial shaft. This creates a deep sulcus between it and the cnemial crest medially. No intercondylar groove is present anteriorly, but a small cleft is found posteriorly. Thulborn (1972: 46) noted a smaller, accessory condyle anterior to the outer in *Fabrosaurus* but *H. tucki* does not have a similar accessory condyle.

The head of the fibula is longer than the outer tibial condyle against which it rests. The fibular shaft narrows progressively and is fused with the tibia; it terminates in a blunt end, about 3 mm in diameter, immediately above the fused calcaneum.

The distal tibiotarsal surface permitted only flexion-extension of the tarso-metatarsus. The joint is a pulley, anteroposteriorly rounded, with lateral and medial ridges which prevented long axis rotation. The depressions for the collateral ligaments are well developed (laterally; the medial astragalar surface is damaged). The joint surface rises 12 mm on to the anterior tibiotarsal surface and about 10 mm on to the posterior. The tibiotarsus of *H. tucki* is remarkably convergent with the tibiotarsus of birds and quite unlike that of other ornithischians.

Muscle markings on the tibia-fibula are obscured by fracturing and the flaking of the outer cortical bone, but some surface features remain (Fig. 19). The cnemial crest received the common extensor tendon. A small vertical rugose area on the posterolateral surface of the fibular head may mark the attachment

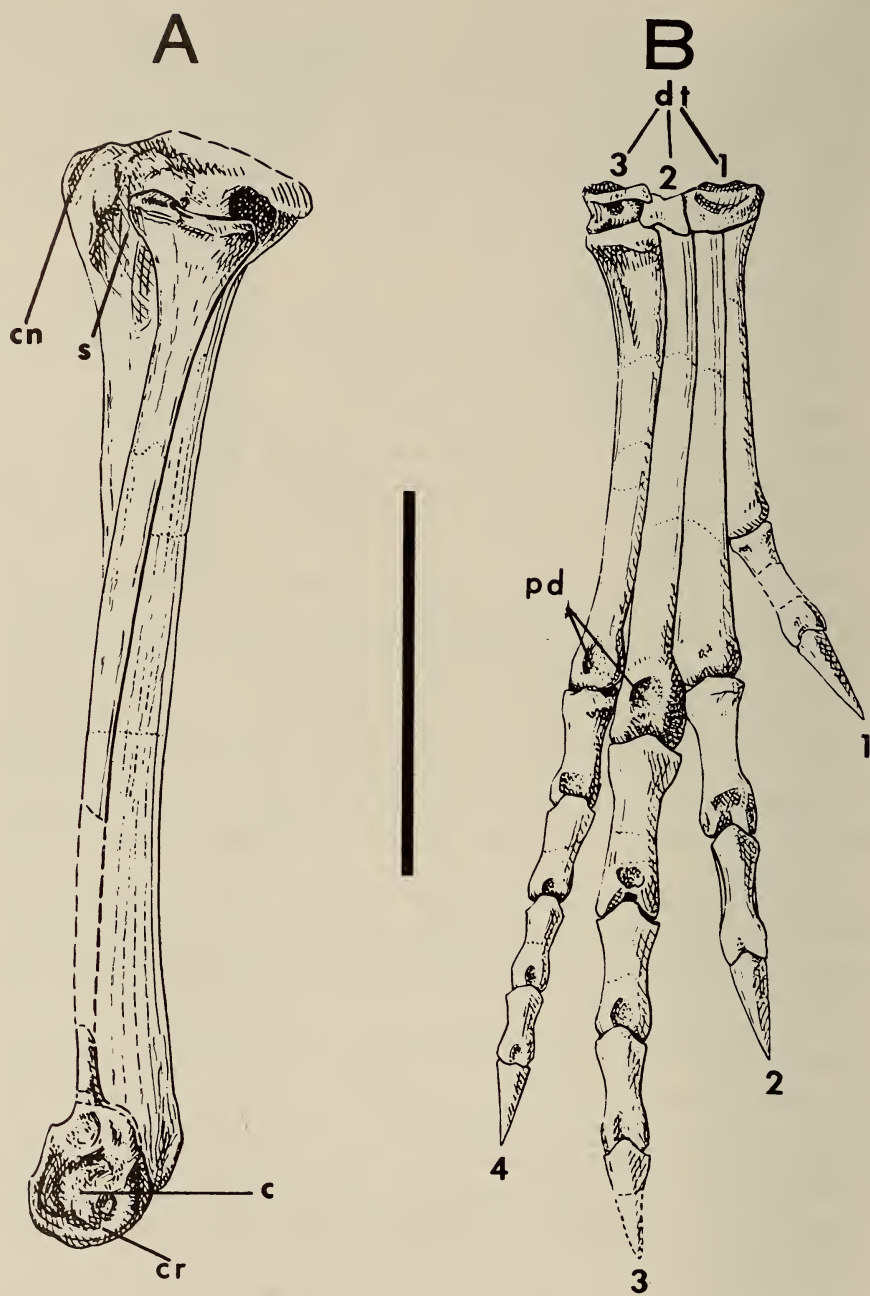


Fig. 20. *H. tucki*. A. Left tibiotarsus, lateral view. B. Right pes and distal tarsals, dorsal view. Scale = 5 cm.



of the ilio-fibularis. Three other ridges can be made out clearly: a vertical ridge on the posterior surface of the fibula, 16 mm below the fibular head and about 12 mm long; a smaller ridge on the lateral fibular surface just below and anterior to the former; another vertical ridge continuous with the second on the edge of the lateral buttress described above. The first may be associated with a head of the digital flexors and the others with the peroneal muscles.

*Pes* (Figs 1, 10C, 20B, 21–22)

The right pes is complete and well preserved save for a transverse fracture proximally and some displacement near the metatarsal bases. The left pes is virtually incomplete except for the phalanges and part of the distal tarsals. The following description, therefore, depends only on the right pes.

The distal tarsals of *H. tucki* differ considerably from those preserved in other ornithischians. In the latter, they are usually flat, disc-shaped bones not ankylosed with the metatarsals. *Fabrosaurus* is similar to other ornithischians in this respect and in no way resembles *H. tucki*. The three distal tarsals of *H. tucki* are fused with each other and with the four metatarsals; the latter are also fused with each other. So just as the tibia–fibula is a structural tibiotarsus, the foot is a structural tarsometatarsus. The fifth digit is only a small splint of bone on the proximoverventral surface of digit 4.

Though fused, the individual tarsals are still distinguishable: distal tarsal 1 caps metatarsals 1 and 2, distal tarsal 2 caps metatarsal 3, and distal tarsal 3 caps metatarsal 4. A ridge rises along the medial and posterior margins of distal tarsal 1; the anterior margin is rounded and the articular surface permitted

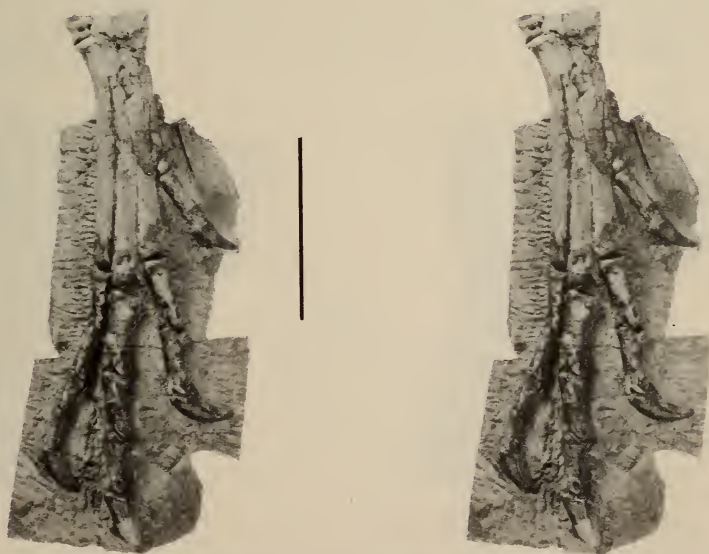


Fig. 21. *H. tucki*. Stereophotograph of right pes and distal tarsals, dorsal view. Scale = 5 cm.

extension of the tarsometatarsus on the tibiotarsus. Posteriorly, the medial edge of the tarsus bears a vertical process or flange (Fig. 10C). The tendon of gastrocnemius may have passed over the tarsus lateral to this tubercle before expanding into the plantar aponeurosis. Distal tarsal 2 also has a rounded anterior margin but a ridge does not appear along the posterior margin; the articular surface is slightly concave. Distal tarsal 3 has a strong ridge round its free margin. The articular surface is a shallow, elliptical depression, antero-posteriorly oriented; this accepts the articular ridge of the calcaneum. The anterior margin of distal tarsal 3 is strongly lipped and overhangs slightly the body of the tarsal; the articular surface thus does not extend on to the dorsal tarsal surface. A foramen pierces the third distal tarsal in the middle of its dorsal (anterior) surface.

The rest of the pes generally resembles a small ornithopod such as *Hypsilophodon*. The head of metatarsal 1 faces medially so the first digit lies in an abducted (i.e. relative to the axis of the pes) position. The first digit was much too short to have been weight-bearing as the tip of the ungual reached only the middle of phalanx 1, digit 2.

The distal articular surfaces of the three weight-bearing metatarsals produce a bird-like stance of the digits. On metatarsals 2 and 4, the surfaces are transversely oblique so both digits were abducted relative to digit 3; on metatarsal 3, the articular surface is horizontal so digit 3 was aligned along the pedal axis. The distal ends of metatarsals 3 and 4 bear a small dorsal pit just above the articular surface; neither metatarsal 1 nor 2 has such a pit. Presumably, digits 3 and 4, being much longer than digit 2, required greater extension to shorten their effective length and allow digit 2 to reach the ground. The dorsal pits on metatarsal 3 and 4 are indicative of this greater extension.

The phalanges of *H. tucki* are characterized by deep interphalangeal pulley



Fig. 22. *H. tucki*. Stereophotograph: detail of right distal tarsals and proximal portion of metatarsals, dorsal view. Scale = 5 cm.

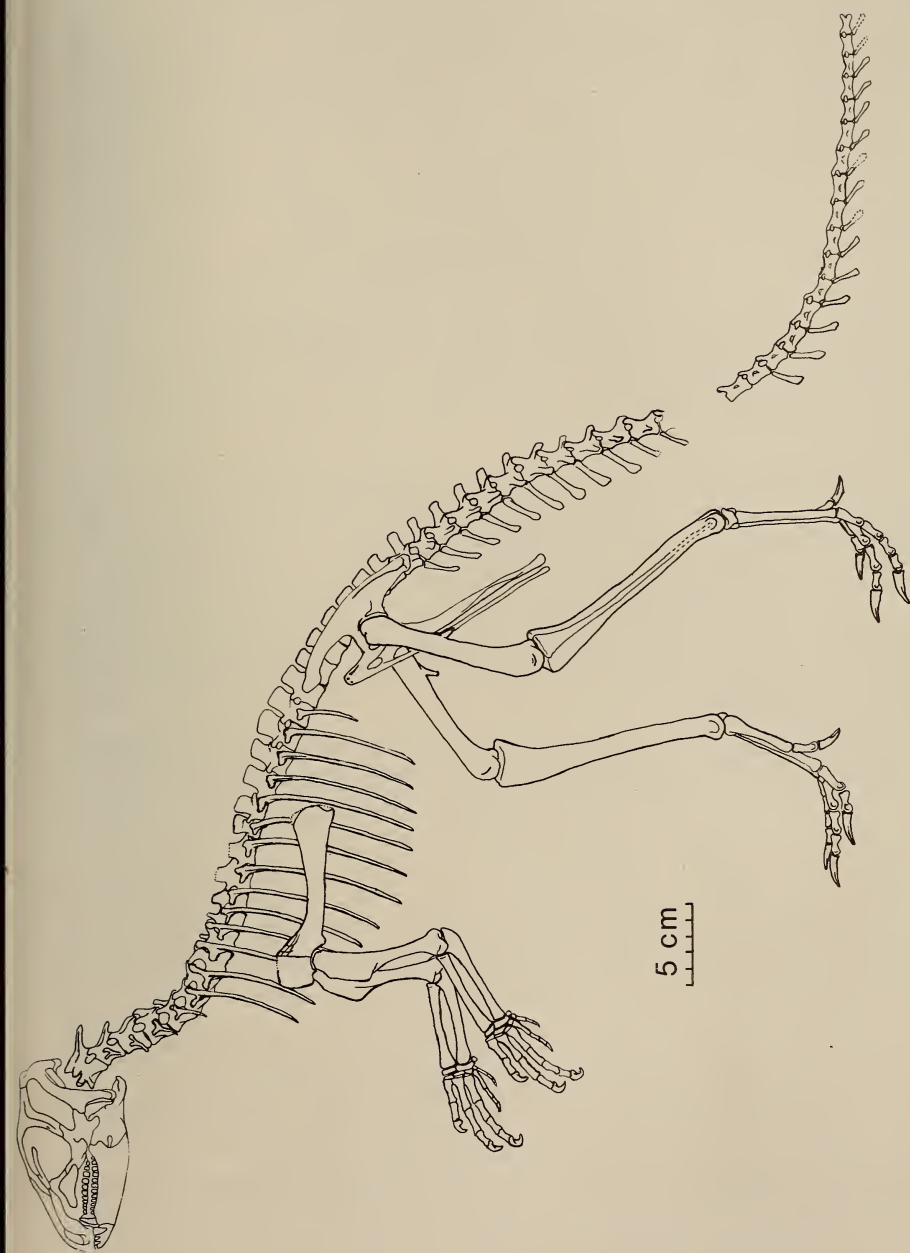


Fig. 23. Reconstruction of *Heterodontosaurus tucki*.



joints. Proximally, a deep intercondylar groove separates the steep-walled condylar articular surfaces; a cross-section of the joint surface here would show a narrow W. A deep pit lies on the dorsum of the phalanx proximal to the articular surface. The condyles are quite extensive; in side view, they describe an arc of somewhat more than  $180^\circ$ . To fit the deep intercondylar groove, the base of the succeeding phalanx has a steep, V-shaped articular surface. The base also has a prominent dorsal keel which reaches the extensor pit of the opposing phalanx. The collateral ligaments were apparently quite robust: a deep pit for the ligament on the lower half of the condyle lies opposite a tubercle for its attachment near the ventral margin of the apposed phalanx.

The terminal joint between ungual and penultimate phalanx differs from the interphalangeal joints only in that the pit for the collateral ligament lies near the dorsal margin of the penultimate phalanx. The ungual phalanges are transversely compressed claws but are not greatly recurved. They have a groove along their length both laterally and medially.

### Comparisons

The ilium of *H. tucki* resembles that of *Hypsilophodon* most closely amongst ornithopods (also that of *Protiguanodon* and *Psittacosaurus* should they be classed as ornithopods). The ilia of *Camptosaurus* and *Thescelosaurus* have a much deeper brevis shelf. Hadrosaur ilia have the dinosaurian antitrochanter which the ilium of *H. tucki* does not have. The ilium of *Iguanodon* differs in having a slightly reflected dorsal supra-acetabular margin and deeper post-acetabular blade. Amongst the non-ornithopods, the ilium of *Protoceratops* is remarkably similar to that of *H. tucki*.

The prepubis of *H. tucki* is similar to that of *Fabrosaurus* and *Scelidosaurus*. The pubis of ornithopods generally has a much longer prepubic process, sometimes associated with a greatly reduced postpubic process (hadrosaurs). A short prepubic process (but with a short postpubic process unlike that of *H. tucki*) can be found in the pelvis of *Psittacosaurus*, *Protiguanodon* and *Protoceratops*.

The ischium of *H. tucki* has few parallels within the ornithopods; it is similar only to *Psittacosaurus*, *Protiguanodon* and the pachycephalosaurs, all of which are doubtful ornithopods. Conversely, all non-ornithopodous ornithischians resemble *H. tucki* in the lack of an obturator process.

The femur of *H. tucki*, with the lesser trochanter not demarcated from the femoral shaft, cannot be matched in any ornithopod. The femora of some ankylosaurs, some stegosaurs (*S. ungulatus* (Gilmore 1914)) and *Triceratops* are similar (the trochanters are separated by a small notch in *Protoceratops*). In this respect, *H. tucki* is more similar to theropod dinosaurs.

In general morphology, the tibia of *H. tucki* resembles that of *Hypsilophodon* and *Fabrosaurus*. However, the fusion of tibia-fibula and astragalus-calcaneum into a functional tibiotarsus does not seem to have an equivalent within the ornithischians.

The pes of *H. tucki* is less distinctive than the tibiotarsus and similar to that

of many light ornithopods: *Fabrosaurus*, *Hypsilophodon*, and *Dryosaurus* (Galton 1977). The pes also resembles that of *Thescelosaurus* and *Camptosaurus* in the closely applied proximal metatarsals; but these heavy bipedal forms have proximodistally compressed phalanges unlike those of *H. tucki*. Outside the ornithopods, the pes most closely resembles that of *Microceratops* and to a lesser extent that of *Protoceratops*.

## DISCUSSION

### *Diagnosis*

#### Order ORNITHISCHIA

#### Suborder incertae subordinis

#### Family *Heterodontosauridae* Romer, 1966; Kuhn, 1966

The following diagnosis of *Heterodontosaurus tucki* Crompton & Charig, 1962, is based on the postcranial skeleton of SAM-K1332: short presacral column of 21 vertebrae (9 cervical + 12 dorsal), sacrum with 6 fused vertebrae; at least 34 caudal vertebrae; ossified tendons present in dorsal and sacral region, but absent from caudal. Scapula elongate relative to trunk; humerus with large deltopectoral crest and large entepicondyle; humerus lacks posterior intercondylar fossa; ulna with olecranon process; nine carpal bones, one of which occupies a position analogous to the os centrale; digits 1–3 parallel, digits 4 and 5 reduced and abducted. Ilium with articular boss analogous to avian antitrochanter; prepubis short but deep, postpubis as long as ischium; ischium without obturator process; greater and lesser femoral trochanters not separated by cleft; transverse axis of distal femoral surface obliquely oriented; fibula reduced and fused with tibia; astragalus–calcaneum fused with each other and to the tibia–fibula; three distal tarsals present, all fused to each other and metatarsal heads; metatarsals 1–4 fused.

### *Morphological interpretation*

The functional importance of several morphological features may not be entirely clear from the foregoing descriptions. In particular, the orientation of the vertebral column and the posture of the forelimb and hind limb should be discussed.

In the vertebral column, a strong flexion is induced in the cervical region by the shape of the centra (Fig. 5A). The posterior cervicals are especially important in this: their trapezoidal outline combined with their shortness creates an abrupt flexion at the transition from dorsal to cervical region. Secondly, ossified tendons are present only in the dorsal region of the vertebral column; the back was therefore a rigid structure, the ossified tendons presumably acting to resist flexion and support the trunk during bipedal progression. Thirdly, the tail of *H. tucki* was not strengthened by ossified tendons. This is probably not a vagary of preservation since the caudals are by far the best

preserved vertebrae. Consequently, the tail was not a rigid structure as inferred for some other ornithischians such as *Hypsilophodon* and hadrosaurs, but was flexible and mobile.

The hind limb of *H. tucki* cannot be articulated at a right angle to the long axis of the ilium. The presence of the avian-like antitrochanter required the femoral long axis to lie at 45° or less to the iliac long axis. In normal resting position, the femur would thus be protracted. There is a further similarity to birds since the femur must also be abducted relative to the midsagittal plane. This clearly follows from the oblique orientation of the inferior femoral surface: only in abduction of the femur would the femorotibial joint of *H. tucki* be horizontal and thus stable. This is completely analogous to the structure of birds in which the inferior femoral articular surface is also oblique. It might be argued that since known dinosaur trackways are narrow, the hind limb could not have been abducted in any dinosaur. However, it must be remembered that in birds, in spite of femoral abduction, rotation about the knee joint of the supporting limb brings the body weight over this limb and close to the centre of gravity, creating a narrow trackway. A similar system is to be expected in *H. tucki* because of the very close structural similarity to the avian hind limb and joint surfaces.

Many features of the forelimb can be interpreted as quadrupedal adaptations; however, the evidence is not unequivocal. As already noted, the ulna of *H. tucki* has a relatively large olecranon process. Such a feature is usually considered a quadrupedal adaptation since it increases the lever arm of the ulna; indeed, the forelimb itself is relatively large compared to that of *Fabrosaurus* and *Hypsilophodon*. The large entepicondyle of the humerus indicates powerful forearm flexor and rotational musculature, a further sign of quadrupedal capabilities. In addition, presence of a large entepicondyle has been interpreted by Bakker (1971) as a key feature in the sprawling gait of primitive tetrapods. Finally, the large flexor tubercle of the unguals may be associated with a powerful propulsive stroke during push-off. Thus the forelimb of *H. tucki* quite clearly had the structure requisite for quadrupedal locomotion.

However, each trait may also be interpreted as a feature of a powerful, grasping manus. In the case of a manipulative hand, the skeletal features associated with forelimb flexion would also be emphasized. Only the olecranon process does not seem to fit this interpretation; yet, the coelurosaur *Syntarsus* (Raath 1969) has a grasping hand and also an elongate olecranon. Furthermore, it is quite possible that the forelimb and hand of *H. tucki* performed a dual function, in locomotion and feeding, as in living sciurids.

Unfortunately, the orientation of the forelimb in *H. tucki* cannot be precisely determined. The humeral head is smooth and rather amorphous and the glenoid is somewhat saddle-shaped. Haines (1952) has pointed out that in living reptiles the ligaments surrounding the shoulder joint, not the joint surfaces themselves, are primarily responsible for determining the range of humeral movements. The long axis of the scapula would have been more or less



parallel to the vertebral column, as found in articulated skeletons of hadrosaurs; consequently, the long axis of the glenoid would have been horizontal. The lack of a posterior intercondylar groove on the humerus is most unusual since that would have severely restricted forelimb extension. Furthermore, the extent of forelimb rotation which would have been possible is indeterminate: the radial condyle of the humerus is not rounded but ellipsoid or ridge-like; this would seem to restrict rotation, yet a similar condylar structure in *Sphenodon* permits about 45° pronation/supination (Haines 1946). The orientation of the humeral condyles is similar to those of *Sphenodon* and *Varanus*; thus, even with 45° rotation the humerus of *H. tucki* would have to have been abducted somewhat (approaching a semi-sprawling position) for the palmar surface of the manus to contact the ground. Thus, a fully erect gait (as described by Bakker 1971) is questionable for the forelimb of *H. tucki*.

### *Heterodontosaurus* and *Fabrosaurus*

The extent of the difference between these two genera must be appreciated for an understanding of ornithischian phylogeny (see Table 1). *Heterodontosaurus* and *Fabrosaurus* represent a schism in ornithischian structure which cannot be contained within a single family. A whole series of anatomical characters separates these genera, many of which reflect the differences in ornithopods and non-ornithopods of the Jurassic-Cretaceous.

These distinctions are important because Galton (1978: 154) has contended that fabrosaurids were either directly or indirectly ancestral to heterodonto-

TABLE 1

Differences in the postcranial skeleton of *H. tucki* and *Fabrosaurus* (Thulborn 1972)

Feature	<i>H. tucki</i>	<i>Fabrosaurus</i>
forelimb and hand	relatively and absolutely larger	relatively and absolutely smaller
humerus	posterior intercondylar groove absent	posterior intercondylar groove present
humerus	entepicondyle large	entepicondyle absent
ulna	olecranon process present	no olecranon process
ilium	posterior process shallow	posterior process deep
ilium	presence of 'avian antitrochanter'	dorsal acetabular margin roofed
ischium	obturator process absent	obturator process present
trochanters	greater and lesser continuous	greater and lesser divided by cleft
fourth trochanter	rod-shaped	triangular, blade-like
femoral condyles	no intercondylar grooves	posterior intercondylar groove only
tibia-fibula	fused	separate
proximal tarsals	fused to each other and tibia-fibula	separate
distal tarsals	fused to each other and metatarsal heads	separate
proximal metatarsals	square in X-section	lateromedially compressed
ossified tendons	absent in caudal region	present in caudal region

saurids. However, he offered no anatomical comparisons to substantiate how such a derivation could have occurred. When the distinctions listed in Table 1 are taken into account, it would be almost impossible to derive *H. tucki* from a fabrosaurid: the smaller forelimb skeleton, the acetabular morphology, the obturator process, the configuration of the femoral trochanters make *Fabrosaurus* a most unlikely ancestor for *H. tucki*. However, a more primitive heterodontosaurid, without the specializations of *H. tucki* (e.g. without the caniniform teeth, without the jugal boss, without the functional tibiotarsus and tarsometatarsus) could be ancestral to the fabrosaurids or hypsilophodonts.

It also follows from the above distinctions that *H. tucki* is not a hypsilophodontid as Thulborn (1970a, 1970b, 1971a, 1971b, 1972) has previously contended. The absence of the obturator process is alone sufficient to distinguish unequivocally the two forms. The taxonomic significance for ornithischians of differences in pelvic structure cannot be ignored. Yet, Thulborn and Galton have done precisely this, the former in trying to make *H. tucki* a hypsilophodontid, the latter in trying to derive *H. tucki* from a fabrosaurid.

#### *The importance of H. tucki*

The distinctions between *Fabrosaurus* and *H. tucki* and the improbability that the latter evolved from a fabrosaurid have important implications for ornithischian evolution. Firstly, since *H. tucki* is a specialized ornithischian, particularly in comparison with *Fabrosaurus*, its specialized nature implies a derivation from a more conservative and stratigraphically older ornithischian. *H. tucki* thus implies the existence of an heterodontosaurid-like radiation of which it is a product: that is, a radiation of non-fabrosaurid, non-hypsilophodontid ornithischians. Thus, the distinctions between the ornithopods and the non-ornithopods of the Cretaceous appear in incipient form in the Triassic.

Secondly, the existence of heterodontosaurids discredits the notion of a 'hypsilophodont plexus' (Thulborn 1971b); that is, that hypsilophodonts were ancestral to all other ornithischians, including the major groups of Jurassic-Cretaceous non-ornithopods. Galton recently advanced a similar hypothesis (1978), that the fabrosaurids were ancestral to all other ornithischian dinosaurs. The existence of heterodontosaurids discredits both hypotheses, primarily because the heterodontosaurids themselves cannot be derived from either hypsilophodonts or fabrosaurids. In addition, because heterodontosaurids lack an obturator process but have quadrupedal as well as bipedal capabilities, they are better structural precursors for the later non-ornithopod groups than are fabrosaurids/hypsilophodonts. Thus, though *H. tucki* itself could not be ancestral to a later non-ornithopod such as *Microceratops*, a heterodontosaurid or a derivative of the heterodontosaurid radiation (without the derived specializations of *H. tucki*) is a much more likely ancestor than a fabrosaurid or hypsilophodont. Consequently, the notion of a hypsilophodont plexus or fabrosaurid basal stock should be restricted to the phylogeny of those ornithischians with an obturator process.

*The significance of the obturator process*

The existence of a fundamental evolutionary dichotomy within the ornithischia, based on the presence or absence of the ischial obturator process would be controverted, at least in part, if it could be shown that some non-ornithopod had an ornithopod (*sensu stricto*) ancestry. The case in point is the Ceratopsia. It has been speculated that *Psittacosaurus* and *Protiguanodon* represent the ancestral group (Romer 1966) of the ceratopsians or at least a related group (Maryńska & Osmólska 1975). However, by the definitions proposed in this paper, *Psittacosaurus* and *Protiguanodon* are clearly not ornithopods and their assumed ancestry to ceratopsians proves nothing about a supposed ornithopod ancestry of ceratopsians. Maryńska & Osmólska (1975) even place the psittacosaurids within the suborder Ceratopsia which makes the question of 'ornithopod' ancestry moot.

This, however, merely throws the question back to the origin of psittacosaurids. Thulborn (1971*b*) stated that psittacosaurids resemble hypsilophodonts in postcranial anatomy but gave no specifics. Unfortunately, Thulborn included both heterodontosaurids and hypsilophodonts (*sensu stricto*) in his category Hypsilophodontidae. In postcranial structure, *H. tucki* clearly resembles the psittacosaurids as much as the hypsilophodonts (*sensu stricto*) do. For instance, and most importantly, the psittacosaurids and *H. tucki* lack the obturator process which all hypsilophodonts have; the precaudal vertebral count (27) is reduced relative to *Hypsilophodon* (30) but is the same as *H. tucki*; the ossified tendons of psittacosaurids extend only from the anterior dorsal to the anterior caudal region, not through the entire caudal region as in *Hypsilophodon*; and the tibiotarsus is closely joined, though not united, in psittacosaurids, but completely free in hypsilophodonts and fused in *H. tucki*. At this simplistic level of analysis, psittacosaurids are no more similar to hypsilophodonts than to *H. tucki*.

In a further attempt to derive ceratopsians from hypsilophodonts, Thulborn derived the protoceratopsids from hypsilophodonts on the basis of certain primitive characters, the only one of which he mentioned was the presence of premaxillary teeth. However, such similarities mean nothing since they are symplesiomorphies. Other characters Thulborn used to join ceratopsians with hypsilophodonts also fall into this category, i.e. a nasal-maxilla contact. In fact, no sound evidence exists to support a hypsilophodont (*sensu stricto*) ancestry of ceratopsians in preference to a non-hypsilophodont ancestry.

The existence of a fundamental evolutionary dichotomy within the Ornithischia would also be controverted if it could be shown that the absence of an obturator process were due to secondary loss. However, the hypothesis of secondary loss of the obturator process in non-ornithopod Jurassic-Cretaceous ornithischians is but an assumption; the fact is, no evidence exists that these forms have ever possessed such a process. But the hypothesis will be examined anyway; it will be shown that secondary loss is less plausible than a hypothesis of original absence for several reasons.

Of the five major divisions within the Ornithischia, only the ornithopods



possessed an obturator process; according to the loss hypothesis, therefore, stegosaurs, ceratopsians, ankylosaurs and pachycephalosaurs first possessed and then lost this trait. For a structure which must have had some adaptive significance to develop in the first place, this is a poor record of adaptive value. It could be assumed that the process was lost because it was not necessary for quadrupedal forms but was for bipedal forms. However, if the obturator process were important for bipedal progression, why did it first appear and then disappear in the lineages represented by pachycephalosaurs, psittacosaur, *H. tucki* and *Microceratops* which were all bipedally adapted ornithischians? The most plausible, logical and evolutionarily sound answer is that the obturator process never existed in these forms. According to the loss hypothesis, the only reason the obturator process would have disappeared was that an animal had taken up a quadrupedal mode of locomotion; the bipedal ancestors of these animals should, therefore, have possessed an obturator process. However, in the only test case available, the Ceratopsia, all the related bipedal forms (psittacosaur and *Microceratops*) do not have an obturator process. This is certainly contradictory; it is more plausible to assume that the obturator process never existed in these forms than to assume it was lost secondarily.

The obturator process is clearly related to bipedalism within the Ornithischia since no known quadrupedal form possesses this process. While some bipeds did not have an obturator process, the most successful bipedal ornithischians (in terms of diversity) did have this process. In addition, the only large bipedal ornithischians (e.g. *Iguanodon*, *Camptosaurus* and hadrosaurs) all possessed the process. Bipedal ornithischians without the obturator process, *H. tucki*, *Microceratops*, psittacosaur, and the pachycephalosaurs of Mongolia, are all relatively small dinosaurs. If the obturator process were really functionally important in an efficient bipedal gait in larger animals, then, as descendants of the small bipedal forms increased in size, they assumed a quadrupedal gait. This is presumably what occurred during the evolution of ceratopsians; thus, the lack of an obturator process was not due to secondary loss.

#### *H. tucki* and ornithischian classification

While the ornithischian status of *H. tucki* cannot be questioned, its subordinal classification is problematical. As defined and used, the Ornithopoda are bipedal ornithischians (Romer 1956: 627–628). The inadequacy of placing all bipedal ornithischians within the Ornithopoda has become apparent recently as more varied ornithischian types are discovered and described. For example, both the pachycephalosaurs and *Microceratops* differ greatly from typical ornithopods such as *Hypsilophodon* yet they are certainly bipedal. Should these forms be included in the Ornithopoda, the meaning of this category in terms of representing ornithischian evolution would be almost nil.

*H. tucki* presents the same classificatory difficulty as pachycephalosaurs, *Microceratops*, *Protiguanodon* and *Psittacosaurus*. Since the ancestors of the quadrupedal non-ornithopods were very likely bipeds, as *Microceratops*

indicates for the ceratopsids, then bipedalism is not limited to any one phylogenetic lineage in the Ornithischia but is distributed throughout the various phyletic lines. Consequently, to classify all bipedally adapted ornithischians as ornithopods only confuses the phylogeny of the Ornithischia by creating a paraphyletic group. Since *H. tucki* is phylogenetically divergent from ornithopods such as hypsilophodonts and iguanodonts, then it makes little sense to classify *H. tucki* as an ornithopod. Furthermore, since *H. tucki* could not have been derived from a fabrosaurid, it is even less desirable to classify it as an ornithopod.

However, the real problem here is not *H. tucki*, but rather the definition of the Ornithopoda and this should be dealt with first. The Ornithopoda could be defined as only those ornithischians which possess an obturator process on the ischium. This basic dichotomy in the ornithischians should finally be recognized, particularly since pelvic structure has tremendous taxonomic value for both groups of dinosaurs. The Ornithopoda would thus be defined on the basis of a probable derived character and approximate a natural group much more than under the other definition. The obturator process is usually considered a primitive structure for the ornithischians, while its absence has usually been attributed to loss. However, the converse seems more likely: the obturator process is a new, derived structure, not present in other archosaurs; consequently, the presence of the process must be explained, not its absence. The Ornithopoda thus defined could be placed in two infraorders, one comprising a lineage represented by hypsilophodonts and related forms such as fabrosaurids, the other comprising the lineage represented by iguanodonts and hadrosaurs.

The non-ornithopods such as stegosaurs and ankylosaurs could be included in a single suborder as separate infraorders, but this would define the suborder on the basis of a symplesiomorphy (lack of an obturator process) and would not be equivalent to the suborder Ornithopoda. It would be preferable to leave these groups as separate suborders since these can be defined on the basis of derived characters and are thus equivalent to the suborder Ornithopoda.

As a consequence of this redefinition, *H. tucki* is certainly not an ornithopod, yet it does not clearly fit into any other suborder. This should not cause surprise since the cranial and postcranial material for the heterodontosaurids and Triassic ornithischians is still somewhat limited. The family has been known only for a short time; until further material is found which defines the extent of the heterodontosaurid radiation, the family should simply be 'incertae subordinis'. The situation is like that of pachycephalosaurs which were too poorly known to classify for a long time.

## SUMMARY

*H. tucki* was a very small Late Triassic ornithischian dinosaur about 1 m long. The postcranial skeleton combines an elongate hind limb adapted to bipedal locomotion and a moderate but not reduced forelimb adapted to

quadrupedal locomotion and/or grasping movements of the hand. *H. tucki* was undoubtedly a facultative biped; a quadrupedal gait was probably used during slow locomotion, perhaps while foraging. The elbow structure suggests that a semi-sprawling attitude of the forelimb was possible. The pelvic structure indicates that the femur was both abducted and protracted, creating a stance similar to, but not the same as, that of birds.

The hind limb proportions of *H. tucki* show an elongated tibia and metatarsus relative to the femur. This is usually interpreted as a cursorial adaptation (e.g. Galton 1974), though no sound evidential basis exists for this inference. Certainly, to infer cursorial habits in a bipedal reptile from the hind limb proportions of living quadrupedal mammals is questionable. Different taxa have different base levels from which cursorial limb proportions develop; thus, comparisons across groups may mean very little. *H. tucki* may or may not have been cursorial: this inference could only be substantiated by comparisons with the hind limb proportions of other heterodontosaurids; these, however, are presently unknown.

The classification of *H. tucki* within the Ornithischia is complicated by the inadequate definition of the Ornithopoda. Once it is accepted that not all bipeds must be classed as ornithopods, then a better definition can be given based on the presence or absence of the obturator process. *H. tucki* need not be placed in the Ornithopoda; rather, it is taken as a representative of an early non-ornithopod radiation which is presently too poorly known to warrant subordinal or infraordinal distinction. However, if *H. tucki* is representative of other heterodontosaurids, then they are more likely structural and phyletic precursors to at least some non-ornithopods than are the fabrosaurids.

*H. tucki* seems to represent a basic cleavage in the Ornithischia. The only two well-known Triassic ornithischians fall on either side of this division which mirrors the differences in pelvic structure of Jurassic-Cretaceous ornithopods and non-ornithopods. Though *H. tucki* probably represents an early non-ornithopod radiation, it does not itself seem to be ancestral to any known later ornithischian. Similarities with primitive ceratopsians are suggestive but difficult to interpret. Nor does *H. tucki* help in the search for ornithischian origins, because its structure is already typically ornithischian. Its features do not point to any special group in the thecodonts. This implies a considerable but indeterminate independent phylogenetic history for the Ornithischia.

#### ACKNOWLEDGEMENTS

I wish to thank Dr T. H. Barry, Director of the South African Museum, Cape Town, for permission to study the material described here. I am very grateful to Dr A. W. Crompton, Director of the Museum of Comparative Zoology, Harvard University, for the use of the material, permission to photograph it and for many valuable discussions and comments during the preparation of this manuscript. Dr A. J. Charig, British Museum (Natural History),



also offered valuable criticisms. The postcranial material described here was prepared by Mr Arnie Lewis (now of the U.S. National Museum, Washington, D.C.), and by Mr Chuck Schaff and Mr Bill Amaral of the Museum of Comparative Zoology. The skull was prepared at the South African Museum. The drawings were prepared by Ms M. L. Estey at the Museum of Comparative Zoology, Harvard University; the stereophotographs were taken by Mr Alan Coleman, also of the Museum of Comparative Zoology. The photograph of the skull was taken by Mr Neville Eden of the South African Museum. The remaining photographs were prepared by the author. This research was conducted while the author was in the Department of Anthropology, Peabody Museum, Harvard University, and later in the Department of Anatomy, Harvard Medical School. The Department of Cell Biology, The University of Texas Health Science Center at Dallas, provided funds for the completion of the manuscript.

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## ABBREVIATIONS

ap	acromial process
ar	anterior ridge of cervical centra
at	avian-like antitrochanter
C	coracoid
c	calcaneum
ca	capitulum
ch	chevron
cn	cnemial crest
cp	coronoid process
cr	calcaneal ridge
ct	coracoid tubercle
d	diaphophysis
dc	deltopectoral crest
dt	distal tarsal
ee	entepicondyle
f	vertical flange, ventral surface of metatarsals
ft	flexor tubercle
gt	glenoid tubercle
hh	humeral head
if	ischial flange: possible attachment of flexor tibialis internus and ischio-trochantericus
IL	ilium
ir	iliac ridge: attachment of ilio-tibialis and ilio-fibularis
IS	ischium
it	infra-acetabular tubercle: possible attachment of accessorius
mct	metacarpal tubercle
ns	neural spine
odp	odontoid process of axis
op	olecranon process
ot	ossified tendons
p	pubis
pa	parapophysis
pd	pit on dorsal surface of metacarpal or metatarsal
pi	pisiform
pr	posterior ridge of cervical centra
poz	postzygapophysis
prz	prezygapophysis for atlantal neural arch
pt	tubercles on prepubic process
R	radius
r	ridge above radial condyle of humerus
re	radiale
rt	radial tubercle



S	scapula
s	sulcus between cnemial crest and lateral buttress of tibial shaft
t	tuberculum
tf	fourth trochanter
tg	greater trochanter
tl	lesser trochanter
tm	tuberosity medial to humeral head
U	ulna
ue	ulnare
ur	ulnar ridge
vk	ventral keel
vr	ventral ridge delimiting fossa beneath transverse process

## APPENDIX 1

Measurements of the postcranial skeleton of *H. tucki* (SAM-K1332), in mm.

(NA = not available; the lengths of some vertebral centra were determined from radiographs and these are noted in the table; parentheses indicate approximate measurements.)

SCAPULA	LEFT	RIGHT
Max. length . . . . .	86,9	85,1
Max. proximal width . . . . .	26,3	NA
Max. distal width . . . . .	22,3	NA
Min. blade breadth . . . . .	8,2	NA
CORACOID		
Max. length . . . . .	(22)	NA
Max. width . . . . .	(23)	NA
Min. width . . . . .	NA	NA
HUMERUS		
Max. length . . . . .	82,3	83,5
Proximal transverse width . . . . .	NA	20,6
Max. distal width (transverse) . . . . .	21,8	17,1
Least shaft diameter . . . . .	7,5	6,9
Length: deltopectoral crest . . . . .	34,4	35,0
RADIUS		
Max. length . . . . .	(57)	58,5
Max. proximal width . . . . .	NA	9,7
Max. distal width . . . . .	9,4	9,4
Least shaft diameter . . . . .	4,3	4,6
ULNA		
Max. length . . . . .	67,6	67,7
Max. proximal width . . . . .	NA	15,2 (including coronoid process)
Max. distal width . . . . .	7,3	7,6
Least shaft diameter . . . . .	3,6	4,1
Length: base of sigmoid notch-distal end . . . . .	NA	57,3
ILIUM		
Max. length . . . . .	96,9	96,7
Length: anterior end to middle of acetabulum . . . . .	(55)	58,0
Length: posterior end to middle of acetabulum . . . . .	41,9	38,7
Min. height above acetabular rim . . . . .	15,0	14,6
ISCHIUM		
Max. length . . . . .	NA	114,2
Max. height . . . . .	NA	23,0
Least shaft diameter . . . . .	3,9	3,7
PUBIS		
Max. length . . . . .	NA	125,7
Height at anterior end of prepubic process . . . . .	NA	7,8
Length: to anterior wall of obturator foramen . . . . .	NA	15,2
Length: from anterior wall of obturator foramen to distal end . . . . .	NA	110,5
FEMUR		
Max. length . . . . .	112,2	112,0
Proximal transverse width . . . . .	NA	NA
Distal transverse width . . . . .	20,1	20,0
Least shaft diameter . . . . .	NA	9,3
Max. proximal A-P width . . . . .	15,9	17,3
Max. distal A-P width . . . . .	23,8	NA

FEMUR ( <i>cont.</i> )	LEFT	RIGHT
Distal attachment of 4th trochanter to proximal end of femur . . . . .	46,1	NA
Length of 4th trochanter . . . . .	9,8 (broken)	14,0

TIBIA		
Max. length . . . . .	(144)	145,0
Max. proximal transverse width (without fibula) . . . . .	NA	11,7
Max. distal transverse width . . . . .	19,8	22,3
Max. proximal A-P width . . . . .	30,6	NA
Max. distal A-P width . . . . .	15,7	13,9
Least shaft diameter . . . . .	8,9	8,3

## MANUS—RIGHT

DIGIT I	MC		Ph 1		UNGUAL	
	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>
Max. length . . . . .	17,5	17,6	16,6	16,5	16,5	18,2
Proximal transverse width . . . . .	8,3	9,1	6,6	NA	4,6	NA
Distal transverse width . . . . .	6,0	NA	4,8	NA	NA	NA
Length along outer curve . . . . .					23	23

DIGIT II	MC		Ph 1		Ph 2		UNGUAL	
	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>
Max. length . . . . .	23,3	NA	15,6	15,1	16,7	NA	(18)	NA
Proximal transverse width . . . . .	6,0	5,3	6,1	NA	5,0	NA	4,0	NA
Distal transverse width . . . . .	6,6	NA	5,1	NA	4,2	NA	NA	NA
Length along outer curve . . . . .							(21)	NA

DIGIT III	MC		Ph 1		Ph 2		Ph 3		UNGUAL	
	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>
Max. length . . . . .	21,4	22,4	14,1	13,0	12,1	12,6	NA	15,1	NA	17,0
Proximal transverse width . . . . .	5,8	5,7	6,2	NA	4,7	NA	4,1	NA	3,6	NA
Distal transverse width . . . . .	6,4	NA	5,0	NA	4,2	NA	NA	NA	NA	NA
Length along outer curve . . . . .									NA	(20)

DIGIT IV	MC		Ph 1		Ph 2		UNGUAL	
	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>
Max. length . . . . .	14,5	(15)	6,8	6,6	4,6	4,6	2,7	NA
Proximal transverse width . . . . .	4,8	5,8	NA	3,3	NA	2,6	1,8	NA
Distal transverse width . . . . .	3,7	3,8	NA	2,6	NA	NA	NA	NA

## PES—RIGHT ONLY

DIGIT I	MT	Ph 1	UNGUAL	
Max. length . . . . .	38,1	17,3	17,6	
Proximal transverse width . . . . .	NA	NA	NA	
Distal transverse width . . . . .	6,1	4,7	NA	
Length along outer curve . . . . .			20	
DIGIT II	MT	Ph 1	Ph 2	UNGUAL
Max. length . . . . .	59,1	19,4	15,5	20,9
Proximal transverse width . . . . .	NA	NA	NA	NA
Distal transverse width . . . . .	(8)	NA	NA	NA
Length along outer curve . . . . .				24



DIGIT III	MT	Ph 1	Ph 2	Ph 3	UNGUAL
Max. length . . . . .	67,9	21,8	15,6	14,4	(18)
Proximal transverse width . . . . .	5,9	(9)	7,8	6,7	(5,5)
Distal transverse width . . . . .	8,9	7,4	6,5	5,7	NA
Length along outer curve . . . . .					(20)

DIGIT IV	MT	Ph 1	Ph 2	Ph 3	Ph 4	UNGUAL
Max. length . . . . .	61,4	16,8	12,2	10,6	9,7	16,0
Proximal transverse width . . . . .	(6)	NA	6,2	5,5	5,0	NA
Distal transverse width . . . . .	(6)	5,9	5,9	5,0	NA	NA
Length along outer curve . . . . .						18

## VERTEBRAL COLUMN

Vertebra No. Presacrals	Max. length of Centrum	Vertebra No. Sacrals	Max. length of Centrum
Axis	16,2	1	14,2
3	14,2	2	(13)
4	15,9	3	NA
5	(15,5)	4	NA
6	13,4	5	NA
7	13,0	6	14,2
8	13,1	Caudals*	
9	NA	A1	14,2
10 (x-ray)	(13)	A2	NA
11	13,2	A3	14,8
12	13,5	A4	(15)
13 (x-ray)	(13)	A5	15,5
14 (x-ray)	14,5	A6	15,8
15 (x-ray)	15,2	A7	16,0
16 (x-ray)	15,0	A8	17,0
17 (x-ray)	15,1	A9	17,8
18	14,8	A10	17,8
19	NA	A11	18,2
20 (x-ray)	(15)	A12	fragmentary
21	14,6		

\* Sequentially numbered on each block of matrix, A and B.

Vertebra No. Caudal	Max. length of Centrum
B1	16,0
B2	16,0
B3	16,2
B4	16,5
B5	16,4
B6	16,7
B7	16,3
B8	16,3
B9	16,3
B10	17,1
B11	16,4
B12	16,0
B13	NA
B14	15,5
B15	15,6
B16	fragmentary